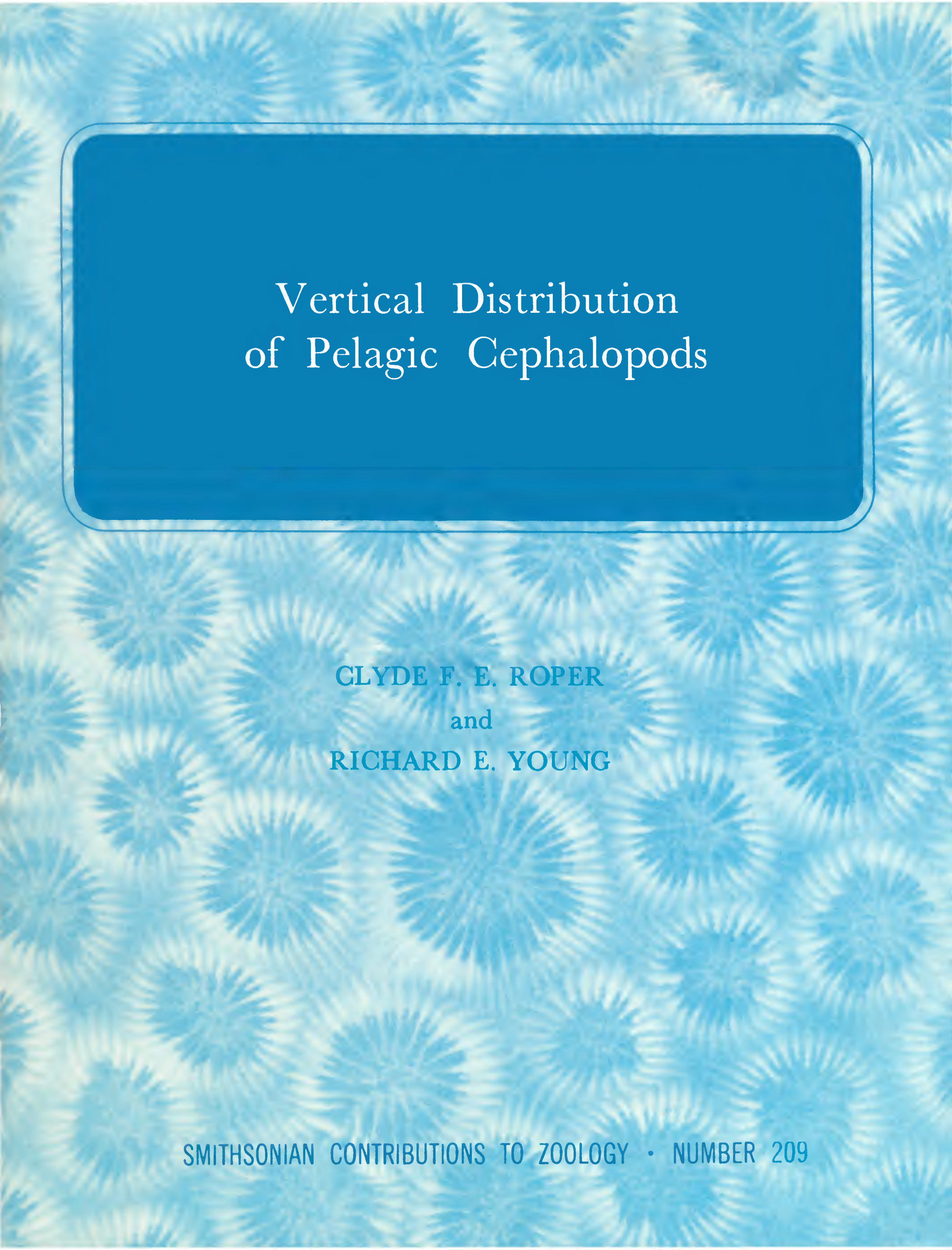

Vertical Distribution of Pelagic Cephalopods

CLYDE F. E. ROPER
and
RICHARD E. YOUNG

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 209

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ABSTRACT

Roper, Clyde F. E., and Richard E. Young. Vertical Distribution of Pelagic Cephalopods. *Smithsonian Contributions to Zoology,* number 209, 51 pages, 31 figures, 1975.—The vertical distributions of pelagic cephalopods are analyzed, based primarily on studies undertaken in the waters off California, Bermuda, and Hawaii. Much of the information is derived from midwater trawl nets equipped with closing apparatus. Each family that contains pelagic or quasi-pelagic species is discussed; selected records from the literature are included where necessary.

A wide variety of patterns of vertical distribution exists among pelagic cephalopods; patterns may be associated with stage of maturity, diel rhythms, or seasonal behavior. The study revealed that several basic types of vertical distributional patterns occur: near-surface dwellers, first order diel vertical migrators, second order diel vertical migrators, diel vertical shifters, diel vertical spreaders, nonmigrators, vertical wanderers, species associated with the ocean bottom, species exhibiting ontogenetic descent.

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Contents

Vertical Distribution of Pelagic Cephalopods

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Introduction

Information concerning the vertical distribution of pelagic cephalopods is relatively sparse. Several factors are primarily responsible: (1) Oceanic cephalopods are often large, fast-swimming animals that are able to avoid being captured by conventional sampling gear. (2) Until recently, most specimens were taken in open nets that, in addition to the desired sampling depth, sample the entire water column during setting and retrieval; as a result the true depth of capture is difficult to define precisely. (3) In many groups only larvae and juveniles are captured and adults are rare or unknown. (4) Most sampling has been conducted along geographical transects where a given locality is generally sampled only once, at one time of day and at one season of the year. Compounding these sampling problems are the complexities of the distributional patterns of the cephalopods.

To understand the vertical distributions of cephalopods (as indeed of many oceanic organisms) a knowledge is required of more than merely the bathymetric range, with carefully defined upper and lower limits, over which specimens of a species are known to occur. Often the bathymetric range will extend over a great vertical distance, but the vast majority of a population will occupy only a restricted depth zone. In addition, larvae of a species may inhabit one or more depth zones that are uninhabited by adults. Therefore, because distributional patterns often differ markedly between growth stages, it is necessary to separate and distinguish between depth records of larval and juvenile-adult populations. Seasonal or daily differences in depth distributions also may occur; for example, some species migrate to nearshore waters in the summer to feed and/or spawn, then migrate into deeper, offshore waters during winter; many species in the day inhabit depths that differ from their nighttime depths. Because of these factors, it is extremely difficult to draw conclusions from most of the literature.

A factor that has led to considerable confusion in the literature is the inability of many workers to recognize the phenomenon of diel vertical migration in which animals ascend toward the surface zone at night and descend to deeper water during the day. Although vertical migrations are well documented in several groups of pelagic animals, evidence of this phenomenon in cephalopods has been inconclusive until recently. The first indication of vertical movements of cephalopods was given in 1841 by d'Orbigny who noted that cephalopods occurred at the surface at night but were absent during the day (vide G. L. Voss, 1967:511). Similar observations have been recorded since that time. For instance, Sasaki (1914:92) stated that *Watasenia scintillans* comes to the surface at night, where it may be captured by fishermen, and disappears to greater depths during the day. More recently Pearcy (1965) presented trawling data to suggest that some oceanic species show greater frequencies of occurrence in the surface layer

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(0–200 m) during night than during the day, while in the layer of 0–500 m abundance of these species is greater during the day than during the night. Clarke (1969) compared day-night captures using several different types of sampling gear, among them a closing-net, during the SOND cruises in the eastern tropical Atlantic. His results indicate more clearly the existence of vertical migration.

Our studies presented here confirm the occurrence of vertical migration in cephalopods and indicate that this phenomenon is widespread in oceanic squid. These conclusions have relied most heavily on sampling programs conducted in three different oceanic regions of the world. The first study was conducted off southern California by the University of Southern California and involved approximately 900 hours of sampling using open midwater trawls. The second study, known as the Ocean Acre Program, was conducted off Bermuda by the Smithsonian Institution in cooperation with the University of Rhode Island and the U.S. Navy. This study was based upon the use of closing midwater trawls. Projects off Hawaii using closing trawls and open trawls yielded additional information.

This paper reviews the vertical distribution of cephalopods and relies heavily on information derived from the above programs. Much of our data is based on the capture of juvenile specimens. In most species examined, however, juveniles appear to exhibit the same distributional patterns as the adults. Therefore, in most cases, this data can be considered representative of the species.

The larvae of most species of pelagic cephalopods occur in the near-surface waters both during the day and at night and as such do not demonstrate the same distributional patterns as their juvenile and adult forms. In order to determine the distributions of juveniles and adults, therefore, the larvae for each species must be eliminated from the calculations. All specimens that were equal in size (mantle length) to, or smaller than, the largest "larva" captured in near-surface waters during the daytime (indicative of nonmigratory behavior) were eliminated from the calculations.

We have attempted to include pertinent information from the literature. Our treatment of the literature, however, has not been exhaustive because of the problems discussed above, as well as of the danger of interpreting data based on records about which we have no knowledge of the circumstances related to the capture.

The vertical distribution of cephalopods is surveyed by discussing representative species in each family. Knowledge is insufficient to allow a presentation based upon recognized distributional patterns or vertical faunal zones in the open ocean. The systematic approach allows us to present data wherever they exist without having to force them into distributional concepts. Hopefully, within the next few years it will be possible to discuss vertical distribution of cephalopods in relation to the physical and biological parameters of the pelagic environment.

In addition to these primary sources listed above we have utilized data from: (1) a closing-net program in the Mediterranean (Roper, 1974); (2) open midwater trawl sampling of the Antarctic Research Program; (3) bottom trawl surveys in the tropical western Atlantic (National Marine Fisheries Service); (4) a survey with a large, open Engel trawl (WALTHER HERWIG); and (5) our collections from various other areas.

The Ocean Acre and Hawaii data presented here are partial results of continuing programs. The data represent some of the information that was accumulated through January 1972.

For representative illustrations of the various groups of pelagic squid discussed in the following report, the reader may consult Roper, Young, and Voss (1969).

The vertical distributional data are summarized in Figures 24–31. As the graph generalizes data, it should be used in conjunction with the text. The distributions are represented by bars, and only reference to the text will indicate the number of data points available and consequently the reliability of the suggested distributions. Not all species mentioned in the text are included in the graph. The families included in the graph are not necessarily in the same order as in the text.

The following symbols are used in Figures 24–31. Solid bar: distribution of animals not associated with bottom, based primarily on midwater tows. Bars represent centers of distribution where the vast majority of the population occurs. Hachured bar: distribution of animals associated with bottom, based primarily on bottom trawls. Dotted bar: presumed zone of distribution based on limited data. Horizontal dotted line: distributional boundary uncertain. Horizontal dashed line: single open-net record. Solid vertical line (or narrow hachured bar): total distributional range occupied by very small portion of population. Dashed vertical line: few data points scattered over broad range of depths; resolution of actual distribution not possible.

Plots for most species show distributions for day (D) and night (N). Where data indicate no day-night differences, they are combined. Since a few species show seasonal changes, their summer-winter (S-W) distributions are plotted. Data for ontogenetic differences in distribution are also plotted where available. "S→" indicates increasing size of non-adult specimens.

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Materials and Methods

CALIFORNIA STUDY

Material from California was collected by the University of Southern California over a six-year period from 1960 to 1966. During the program, 445 midwater tows were made with an open Isaacs-Kidd midwater trawl representing over 900 hours of "fishing" at depths from the surface to about 1200 m (Figure 1). The program yielded over 5000 specimens of pelagic cephalopods. The systematic study of these cephalopods, including the descriptions of a number of new species, was published by Young (1972a).

The reconstruction of the vertical distribution of the species integrates catches over the entire sampling period. Probably, at any given time the vertical extent of these distributions is considerably less than shown. A correction factor that compensates for unequal trawling time at each depth interval has been added to the charts of vertical distribution (white bars). The correction factor represents the catch that would be expected if all depth intervals were sampled as intensively as the most heavily sampled depth. The actual catch (black bars) is presented on the same chart as the correction factor. This technique is useful when low numbers of specimens are available. Because of the low numbers, the actual catch is discussed rather than the adjusted catch except in a few cases where the adjusted catch gives a slightly different picture of the vertical distribution.

Trawling times generally varied between two and four hours; deep tows generally spent four hours at depth. Any tow that was in the water at 0600 hours or at 1800 hours is considered a twilight tow. For example, if a deep tow began at 0115 hours and terminated at 0615 hours, it is classified as a twilight tow and is excluded from the day-night analyses.

The depth limit of the sampling program was approximately 1200 m. A number of tows undoubtedly extended below 1200 m; because it is difficult to determine actual fishing depth of the net, all specimens caught in tows below 1200 m are lumped into the 1100–1200 m depth zone in the charts. The data are handicapped by occasional lack of precise depth of capture records. In these cases, depth of capture was considered to be one-third of the wire out. This factor was determined by plotting values of wire out against trawl depths that were obtained from a series of trawl hauls with a depth recording instrument present. The localities of trawling stations off southern California are given in Young (1972a).

The oceanographic regime off southern California is unusually complex. The continental borderland, 80–257 km in width from the shoreline to the continental slope, contains 12 complete basins, ranging from about 500–2100 m in depth, several troughs, numerous banks and eight islands. At the western edge of the borderland, the continental slope drops steeply to a depth of about 3500 m. The waters over the borderland are derived from the complex intermixing of several water masses. Surface waters are influenced by the southerly flowing California Current that is derived largely from Subarctic waters and modified through mixing with Central waters. Surface waters also are modified by wind-induced upwelling that brings nutrient-rich waters to the surface from a maximum depth of 200–300 m. Below

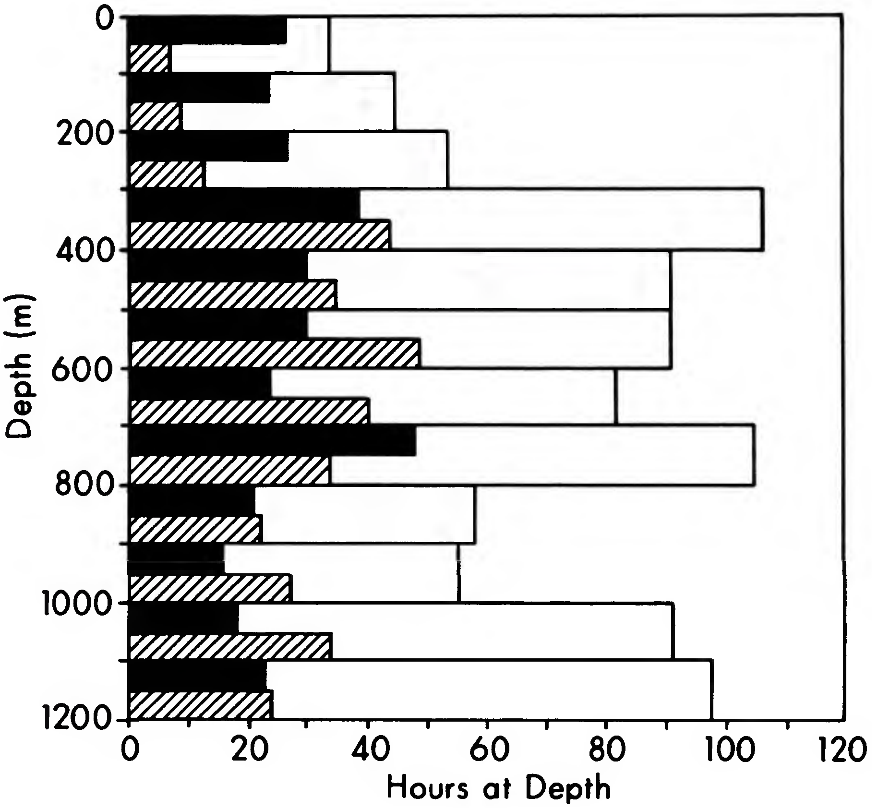

FIGURE 1.—Hours of trawling at various depths (in 100 m increments) off southern California. (Black bar = hours of fishing at night; hatchured bar = hours of fishing during the day; white bar = total hours of fishing (day, night, twilight).)

150–200 m a deep countercurrent of Pacific Equatorial Water flows northward along the coast to at least 40°N and progressively mixes with the lower layers of the California Current. (Above discussion based on Reid, Roden, and Wyllie, 1958; Emery, 1960).

The vertical temperature structure of the water shows considerable variation, often in association with large internal waves (Emery, 1956). In general, however, the average surface temperature varies seasonally from about 14° to 20° C. The 10° C isotherm, which marks the approximate bottom of a strong shallow thermocline, usually lies between 100 m and 200 m. The 8° C isotherm generally fluctuates around the 300 m level, the 6° C isotherm lies between 700 m and 800 m, and the 4° C isotherm occurs at about 1000 m.

Salinity at the surface varies around 33.6 ‰ and gradually increases with depth to about 34.5 ‰ at 1000 m.

Oxygen concentration at the surface is approximately 6.0 ml/L, and between 500 m and 1000 m it reaches a minimum that is less than 0.5 ml/L. Emery (1960) gives an oxygen value of 0.2 ml/L below sill depth in the San Pedro Basin and 0.4 ml/L below sill depth in the Catalina Basin. Emery and Hülsemann (1962) found that oxygen does not appear to be a limiting factor on the abundance of the benthic megafauna in the Santa Barbara Basin in concentrations above 0.3 ml/L. Almost no megafauna was present, however, in less than 0.1 ml/L. A rich cephalopod fauna occurs in the oxygen minimum zone; and no correlation is apparent between the patterns of vertical distribution of cephalopods and the oxygen minimum layer.

Bermuda Study

The cephalopod data utilized here from off Bermuda are part of a study known as the Ocean Acre Program. Details of the long-term program are given in Gibbs and Roper (1970) and Gibbs, Roper, Brown, and Goodyear (1971).

The principal sampling gear was a 3 m Isaacs-Kidd midwater trawl (3 m IKMT) equipped with a cod-end closing device. The four-chambered, electronically actuated sampler is described in detail by Aron, Raxter, Noel, and Andrews (1964). The apparatus allows the collection of three discrete samples at a precise depth and a fourth sample during retrieval of the net from fishing depth to the surface. The gates that separate the chambers are closed by means of a solenoid-actuated triggering mechanism.

The experimental design for Ocean Acre included a regime of depths and times for seasonal discrete-depth sampling. Twelve standard depths were established for sampling the water column during each cruise; each depth was sampled at least once during full daylight hours and once during the night. Trawls that occurred one and one half hours before and after sunset and sunrise were considered to be twilight tows.

The Ocean Acre study area is located east of Bermuda and encompasses a 1° square area centered at 32°N, 64°W. The site has relatively simple oceanographic characteristics, at least in comparison with other deep-water localities in the western Atlantic. The depth of the water in Ocean Acre ranges from about 2000 m in the northwest corner to 4500 m in the southwest region. The physical oceanography is summarized here from Gibbs and Roper (1970:120).

The Surface Water Mass occupies the upper 600 m; surface temperatures range from 20° to 29° C and salinity generally is above 36.4 ‰. A seasonal shallow thermocline occurs between 50 m and 150 m during April to November, with a peak intensity in August. A temperature reduction of 8° C can occur within the thermocline in a vertical distance of 50 m. Below the thermocline temperature and salinity remain nearly uniform (18°–19° C and 36.2° ‰) to about 600 m. From about 600–1100 m a permanent deep thermohalocline occurs that is identified as North Atlantic Central Water. Temperature changes from 18° to 6° C and salinity from 36.2–35.0 ‰ over this depth range. Intermediate water is present between 1100 m and 2000 m with temperatures of 5.5° to 4.0° C and a salinity of about 35.0 ‰. Characteristic North Atlantic Deep Water, with temperatures below 3.5° C and a salinity around 35.0 ‰, occurs below 2000 m. Oxygen levels generally are between 4.5 and 5.5 ml/L at the surface and decrease until about 700–900 m, where an oxygen minimum layer occurs with concentrations around 3.5 ml/L. Below 700–900 m, oxygen concentrations again increase to greater than 6.0 ml/L at 2000–3000 m. Characteristics of the sound scattering layer are difficult to define. With a 12 kHz sound source, a weak and variable scattering layer usually is present at 0–150 m during the day, while a deep, strong layer occurs between 400 m and 600 m. At night the scattering layer is very prominent between 0 m and 250 m, and the 400–600 m layer, though diminished and narrower, is still intact.

HAWAII STUDY

In Hawaiian waters the area of study lies about seven miles off the leeward side of Oahu where water depth exceeds 2000 m. Sampling gear was a modified 10′ Tucker trawl with an opening-closing system in the mouth that is actuated by acoustic signals from the ship. An open 3 m Isaacs-Kidd midwater trawl also was used extensively.

Most oceanographic features off Hawaii are very stable throughout the year. The seasonal range in surface temperature is from 23° to 26° C. A weak, shallow thermocline at about 35 m forms during the spring and summer, while a permanent thermocline extends from about 100 m to about 400 m where the temperature is around 8° C. Temperature at 1000 m is 4° C and decreases to 2° C at 2000 m. Surface salinity is between 34.7 ‰ and 35.2 ‰; between 400 m and 500 m a strong salinity minimum occurs (less than 34.2 ‰), which marks the core of North Pacific Intermediate Water. The very homogeneous Pacific Deep Water lies below about 1500 m. Dissolved oxygen falls to a minimum of about 0.7–1.0 ml/L at about 700 m. (Above discussion based on Gordon, 1970).

Subclass NAUTILOIDEA

NAUTILIDAE

FIGURE 24: BARS 1, 2

Nautilus occurs in tropical Indo-Pacific waters. Species of the genus apparently are not truly pelagic, as living specimens generally are captured near the ocean bottom. Specimens commonly are caught in bottom traps, and in captivity they spend most of the day at rest on the bottom of the aquarium and swim chiefly at night (Bidder, 1962; Stenzel, 1957). *Nautilus macromphalus* is caught in shallow water at night and occasionally may be taken at the surface by fishermen (Rancurel, pers. comm.). The maximum depth to which any species of *Nautilus* can descend is uncertain. Denton and Gilpin-Brown (1966:755) estimated that the shell of *N. macromphalus* is sufficiently strong to withstand hydrostatic pressures to a depth of 600 m, while Collins and Minton (1967) showed experimentally that the siphuncular tube can withstand pressures equivalent to 480 m. In New Caledonia *N. macromphalus* occurs at least as deep as 200 m during the day (Rancurel, pers. comm.). Bidder (pers. comm.) captured a female specimen of *N. pompilius* in a trap at 200 m in the Bay of Rabaul, New Britain, off Vulcan Island. The trap had been set on sandy bottom for only a few hours during the daytime. One specimen of *N. pompilius* was obtained by the *Challenger* off Matuku Island, Fiji, in a dredge haul to 576 m (Moseley, 1879: 256), but Bidder (pers. comm.) feels it may have been caught at a shallower depth as the dredge fished up the slope.

Subclass COLEOIDEA

Order SEPIOIDEA

SPIRULIDAE

FIGURE 24: BAR 3

Bruun (1943:23) investigated the vertical distribution of *Spirula spirula* and concluded that it occurs between 200 m and 1750 m, except in areas of upwelling where it is found as shallow as 100 m. Bruun (1955) re-examined the distribution of *Spirula* and maintained that the upper limit as previously determined was correct. He revised his original estimate of the lower limit of occurrence of *Spirula*, and, based on inconclusive data, implied that this limit probably coincides with the 10° C isotherm. In attempting to correlate the 10° C isotherm with geographical distribution Bruun stated (1955:68): "It is obvious that all *Spirula* fall within the regions where the temperature is about 10° C or higher at a depth of 400 m." (Actually, this is not at all obvious from the chart). His use of the term "regions" refers to geographical regions, but this has been interpreted as vertical region, which led to the misconception that the lower limit of the vertical distribution of *Spirula* is 400 m (G. L. Voss, 1967:516). We are left with

Bruun's suggestion that the lower limit is the 10° C isotherm or the lower boundary of what Bruun termed the thermosphere; this would correspond to a maximum depth in some areas of about 700 m (Bruun, 1957:641).

Bruun (1943:10) found that pressures of 40–65 atmospheres (about 400–650 m) imploded *Spirula* shells collected from the beach; he suggested that shells in the living animal might be stronger. Denton and Gilpin-Brown (1971:367) found experimentally that the chambered shells of *Spirula* in the intact animal are able to withstand pressures equivalent to those occurring at around 1700 m.

Recently Clarke (1969) presented data on the vertical distribution of *Spirula* based on 70 specimens captured near the southern end of the Canary Islands. Using an Isaacs-Kidd midwater trawl equipped with a Foxton closing device, he showed that *Spirula* undergoes vertical migration. Clarke found the daytime center of distribution to be at 500–700 m, while at night *Spirula* ascended to 100–300 m. No specimens were taken shallower than 500 m during the day, but a few were captured well below the center of distribution to depths of 950 m.

SEPIIDAE

The sepiids are quasipelagic, generally burying themselves in the bottom during the day and emerging at night to feed. Therefore, they are beyond the scope of this report.

SEPIADARIIDAE, SEPIOLIDAE, IDIOSEPIIDAE

Among these three families, only certain members of the Sepiolidae are wholly pelagic. Within the Sepiolidae, the Rossiniae and the Sepiolinae are benthic or quasipelagic and spend much of the time buried in the substrate (Naef, 1923).

The remaining subfamily in the Sepiolidae, the Heteroteuthinae (Figure 24:4–7) generally possess silvery bands along the lateral surfaces of the mantle and head. This feature in other cephalopod groups is usually associated with a pelagic habit in the zone of light penetration. Little information exists, however, on the actual vertical range of members of the subfamily.

The vertical distribution of the best-known species, *Heteroteuthis dispar,* was studied by Degner (1925) in the Mediterranean Sea. Captures were made in open nets and depths recorded only as meters of wire out. We have considered the depth of capture to be one-half the length of wire out; this method gives a probable maximum fishing depth (see discussion in Bruun, 1943:21). Degner, reporting on 124 specimens, found that 5.6 percent of the specimens were captured above 35 m, 72.5 percent were captured between 35–150 m, and 21.8 percent were captured below 150 m. Unfortunately, the sizes of individual specimens were not reported. They ranged from at least 2–12 mm ML (mantle length), with specimens from about 2–4 mm ML apparently predominating. Most specimens were captured over deep water. Some of the specimens captured below 150 m are very likely contaminants that were caught while the open nets passed through the populated layer.

Clarke (1969:970) has also presented evidence based on closing nets for a shallow living habitat in *H. dispar.* He found that specimens of this species with mantle lengths greater than 2 mm (24 specimens) were captured during daytime at depths of 110–255 m and at night near the surface (0–70 m) to 265 m.

Our closing net captures from the Mediterranean also indicate the shallow occurrence of *H. dispar,* although several specimens were captured as deep as 400–500 m during the day. Four specimens were captured between 150 and 250 m and 10 specimens were captured between 400 and 500 m during the day. At night 16 specimens were taken between 50 and 300 m (size range of all specimens: 3–25 mm ML).

We have scattered observations on mature or nearly mature specimens in two of the remaining four recognized genera in the Heteroteuthinae (*Nectoteuthis, Iridioteuthis, Stoloteuthis, Sepiolina*). We have recorded 12 specimens of *Stoloteuthis leucoptera* taken in five otter (bottom) trawls that fished at the following depths (in meters): 145, 156, 161, 172, 188; one specimen was taken at night in an open midwater trawl that fished at 350–0 m. Six specimens of *Stoloteuthis maoria* were captured during daytime in two otter trawls that fished on the bottom at 420–440 m and four specimens were taken at night in an open midwater trawl that fished from 53–0 m over water

500–575 m in depth. Three specimens of *Nectoteuthis pourtalesi* were taken in two bottom trawls that fished at depths of 394 and 385 m.

Although it is apparent from the above records that *Heteroteuthis* occurs in the upper few hundred meters during both day and night, the full extent of its range is still uncertain. Examination of the photosensitive vesicles of a species of *Heteroteuthis* (*H. hawaiiensis*) has revealed a small group of vesicles similar in size to those of the shallow living *Loligo vulgaris*. This further suggests to us that *Heteroteuthis* is a shallow living animal. The captures of *H. dispar* from 400–500 m in the Mediterranean, however, are difficult to interpret and remain unexplained until more extensive data are obtained.

Although *Heteroteuthis* probably is pelagic throughout its life cycle, the habitats of the species in the remaining genera are much less clear. The rather meager data indicate that at least some of these species occur at rather shallow depths. The preponderance of specimens taken in bottom trawls compared to midwater captures suggests that these species spend considerable time on or near the bottom.

Order TEUTHOIDEA

Suborder MYOPSIDA

LOLIGINIDAE

FIGURE 24: BARS 8–14

Members of the family are primarily neritic; i.e., generally they are not found over deep water and apparently are restricted to waters of the coastal margins and continental shelves (Summers, 1969). Although all of the approximately 50 known species of loliginids have been recorded from shallow water, details of vertical distributions are known for very few species. The records of captures are based primarily on bottom trawls. Summers (1969) records winter captures of *Loligo pealeii* from Georges Bank to Cape Hatteras in depths of 28–366 m with the highest concentration at 110–183 m; in summer the species migrates inshore to spawn and occurs at depths as shallow as a few meters.

Differences in captures during the day and at night in winter suggest that the squid disperse vertically into the water column at night. In late winter *L. pealeii* is concentrated in the canyons of the slope at 100–200 m where water temperatures remain at 9° to 12° C (Vovk, 1969); with warming waters in spring the concentrations move northward and inshore. The northern limit of distribution is about 600 km further north in summer than in winter (Summers, 1969).

Mangold-Wirz (1963:249) records depth distributions of the following species of loliginids from the Catalane Sea: In *L. vulgaris* the depth at which peak abundance occurs (40–120 m) varies seasonally, being shallowest in the spring when adults come inshore to spawn. *Alloteuthis media* exhibits an inshore-offshore migration similar to that of *L. vulgaris*. Total ranges are approximately 20–200 m. Results of exploratory fishing off the northwest African shelf (Porebski, 1970) give an indication of possible diel vertical movement of *Loligo vulgaris*. Bottom trawls fished from 20–280 m yielded positive captures (abundance varied with depth and locality) during daylight hours, but after 1900 hours no *L. vulgaris* were captured in the trawls, indicating that the animals either leave the bottom and disperse into midwater at night, or move to depths that were not sampled. In the English Channel waters near Plymouth *L. forbesi* is taken readily in bottom trawls during the day at 13–104 m, but is absent from tows made at night (Holme, 1974:496).

LaRoe (1967:50) found that *Loligo* (= *Doryteuthis*) *plei* in the tropical western Atlantic generally occurs from the surface to 180 m; *Sepioteuthis sepioidea*, a very shallow living tropical species, is associated with coral reefs and turtle grass, and is recorded from the surface to 21 m. *Lolliguncula brevis* is recorded by LaRoe (1967:84) from 85 m (one capture) to the surface, with the great majority in less than 18 m.

Although many species of loliginids may be seen at the surface at night over shallow depths, the success of capture with bottom trawls suggests that most species live near the bottom during the day.

PICKFORDIATEUTHIDAE

FIGURE 24: BAR 15

This monotypic family, containing only *Pickfordiateuthis pulchella*, has been captured in shallow tropical waters from the surface to 3–4 m (LaRoe, pers. comm.).

Suborder OEGOPSIDA

The great majority of truly oceanic species of cephalopods are included in the Oegopsida. The group is very diversified and contains over half of all families and genera of living cephalopods. Members of the Oegopsida inhabit a wide variety of oceanic habitats. Some live at or near the surface; some undergo diel vertical migrations; some are restricted to the depths; some undergo shoreward seasonal migrations, and some are associated in part with the ocean bottom.

LYCOTEUTHIDAE

FIGURE 25: BAR 1

G. L. Voss (1962:273) suggested that members of the family occupy the zone from 300–600 m. *Oregoniateuthis springeri* is recorded from a single open net (367–0 m).

Lycoteuthis diadema is recorded from seven captures of adults in open nets that fished at (in meters): 366 (2 stations), 403, 589, 1500, 2195, 3000, and two captures of larvae at 46 m and 57 m (G. L. Voss, 1962:275–277). *Lampadioteuthis megaleia* is recorded from one adult taken at night in an open net that presumably did not descend below 200 m (400 m of wire out) and two larvae (Young, 1964).

Selenoteuthis scintillans was previously known from two records: 46 m at night in an IKMT and 0–3290 m (G. L. Voss, 1962:294). Some closing net data on *S. scintillans* are available from off Bermuda (9 specimens, 11–32 mm ML). Five specimens were captured from 610–650 m during the day and four specimens were taken at 90–130 m at night.

Selenoteuthis scintillans apparently undergoes an extensive diel vertical migration. While data on other species are almost completely lacking, we suspect that vertical migratory behavior may be typical of the group.

ENOPLOTEUTHIDAE

FIGURES 2–5, 25: BARS 2–15

Some members of the Enoploteuthidae are among the most commonly caught squids in midwater trawls. Three subfamilies are known, and within each, the assemblage of species shows considerable homogeneity in size and appearance. The subfamily Enoploteuthinae consists of four genera: *Enoploteuthis, Abralia, Abraliopsis,* and *Watasenia.*

We have data from California, Bermuda, and Hawaii on three species of *Abraliopsis.*

Nine hundred and thirty specimens of *Abraliopsis felis* from open nets were examined from California, of which 480 specimens were used in plotting the vertical distribution; the remainder were too small (less than 15 mm ML) or were captured during twilight. During the daytime only two specimens were captured above 300 m; 93 percent of the specimens were captured between 300 and 600 m with a strong peak between 400 and 500 m (Figure 2). The specimens listed below 600 m probably are contaminants. The exact nighttime position of the population is less clear. The specimens (27 percent) located below 500 m probably are contaminants. Seventy-five percent of the remaining specimens are located in the upper 300 m and 62 percent in the upper 200 m. It is uncertain how many of the specimens taken between 200 m and 500 m are contaminants, so it is difficult to put a lower limit on the major portion of the population at night. The data show that *Abraliopsis felis* undergoes a diel vertical migration covering an average distance of over 300 m, ascending from a mean daytime depth of 450 m to a mean nighttime depth of 100 m.

A great disparity exists between the number of specimens captured during the daytime and at night. Perhaps members of this species school during the day and break up into small groups or completely dissociate at night in the shallower water. Trawl data support this suggestion. Trawls that fished at day below 300 m occasionally caught large numbers of *A. felis* (e.g., 93, 63, 54, 44 specimens) while a maximum of eight specimens was taken in a single trawl that fished above 300 m at night.

Pearcy (1965) found that *A. felis* (as *Abraliopsis* sp.) off Oregon shows a greater frequency of occurrence in the surface layer (0–200 m) during the night than during the day; while in the layer of 0–500 m, occurrence is greater during the day than during the night. These data suggest a distributional pattern similar to that for the same species off California.

Off Bermuda, closing-net captures of *Abraliopsis pfefferi* (15–27 mm ML) during the daytime occur at 610–650 m (three specimens) and at night four specimens larger than 15 mm ML were captured at 50–100 m. Therefore an extensive vertical migration also is indicated for this species.

Ten specimens of *Abraliopsis* sp. (9–20 mm ML) off Hawaii were captured in closing nets during the day between 500 m and 600 m. At night 41 specimens (19–20 mm ML) were taken in open nets; nearly 75 percent of these were captured in tows that fished between 50 and 100 m. One specimen (16 mm ML) was taken in a closing net at 60 m.

Information on the other genera in the subfamily is scarce. Berry (1926) recorded *Abralia veranyi* from Madeira; specimens were observed and captured in Funchal Harbor at night during summer, but were absent during the day. We also have dipnetted *A. veranyi* at night in Bahamian waters. A number of specimens of several species of *Abralia* also have been taken at or near the surface presumably at night (Clarke, 1966:170). These observations suggest that species of *Abralia* probably migrate vertically to or near the surface at night and descend during the day.

Off Bermuda *Abralia* is infrequently caught. Two closing trawl captures were made of *A. red-*

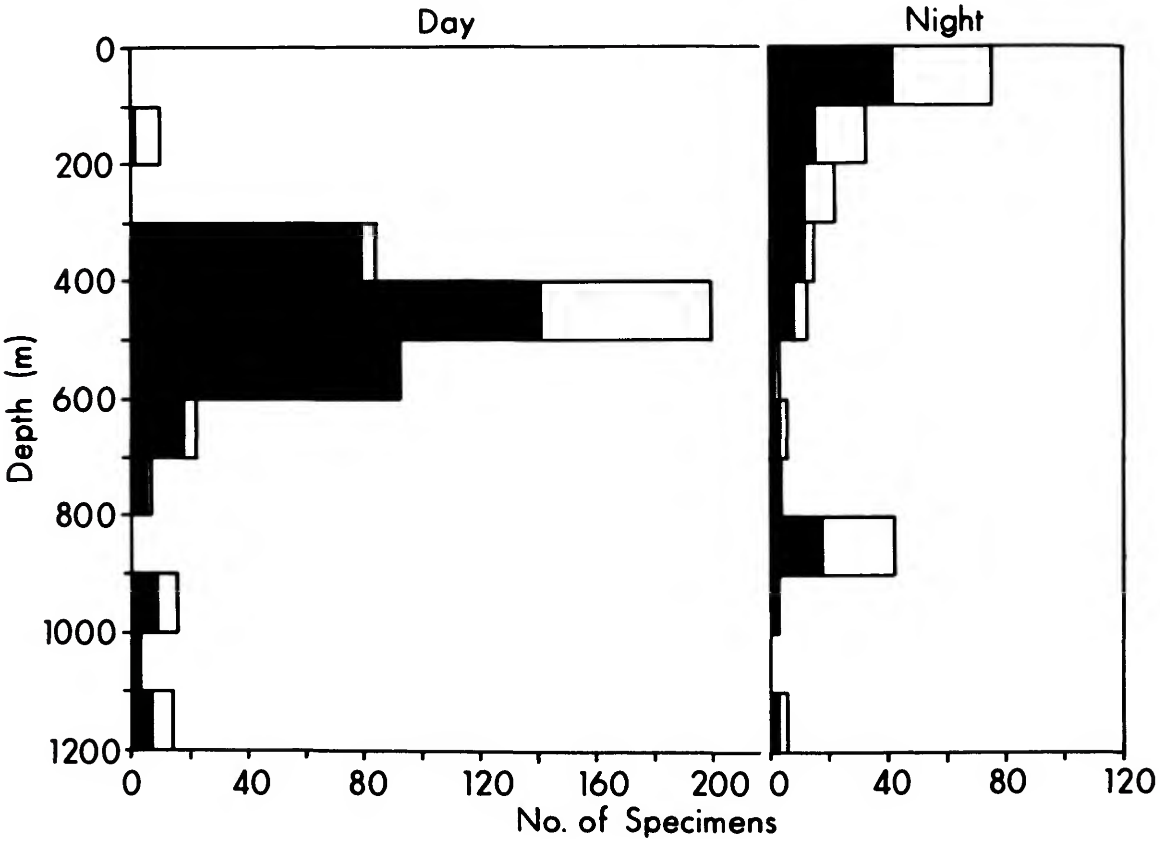

FIGURE 2.—Vertical distribution of *Abraliopsis felis* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

fieldi at night at 50 m. Daytime captures are absent in spite of intensive sampling from the surface to 750 m.

Abralia astrosticta from off Hawaii is known from only a few captures. Although small specimens have been taken in midwaters, most large specimens have been taken in bottom trawls (L. Burgess, National Marine Fisheries Service Laboratory, Honolulu, pers. comm.). One adult (48 mm ML) was taken in a gill net on the ocean bottom at night in 180 m. Extensive pelagic trawling around Hawaii has failed to capture any adults. The meager data suggest that this species may associate with the ocean bottom off oceanic islands.

Off Hawaii three specimens of *A. trigonura* (30–37 mm ML) were captured in a closing net that fished between 460–600 m during the day. In open nets nine specimens (15–37 mm ML) were taken between 490 and 575 m during the day and a single specimen, probably a contaminant, was taken from an open net that fished at 775 m. At night, two specimens (22 mm and 37 mm ML) were captured from 100–0 m.

Sasaki (1914:103) studied the distribution of *Watasenia scintillans* in Japan and concluded that in the spring and summer it lives deeper than 200 m during the day and in the evening it approaches the shore or shallow sea floor to spawn. This is a spawning migration; whether *W. scintillans* in addition undergoes an oceanic daily vertical migration is as yet unknown to us.

Roper (1966) presented capture data on *Enoploteuthis anapsis,* which included six juvenile and adult specimens (17–79 mm ML) that were captured at night between 0–120 m. One Bermuda specimen (15 mm ML) was taken in a closing net at 90 m at night. Three additional specimens of *Enoploteuthis* sp. were taken in closing nets at night; two specimens at 90 m and one at 130 m. No daytime closing-net captures have been made to date.

The Pyroteuthinae contains two genera, *Pyroteuthis* and *Pterygioteuthis. Pyroteuthis margaritifera* is one of the most abundant squids taken in the Ocean Acre program off Bermuda; 163 specimens (5–27 mm ML) were captured in closing nets and their distributions are plotted on a time-depth chart (Figure 3). The boxed digits indicate the number of specimens caught at a given time and depth per hour of trawling throughout the

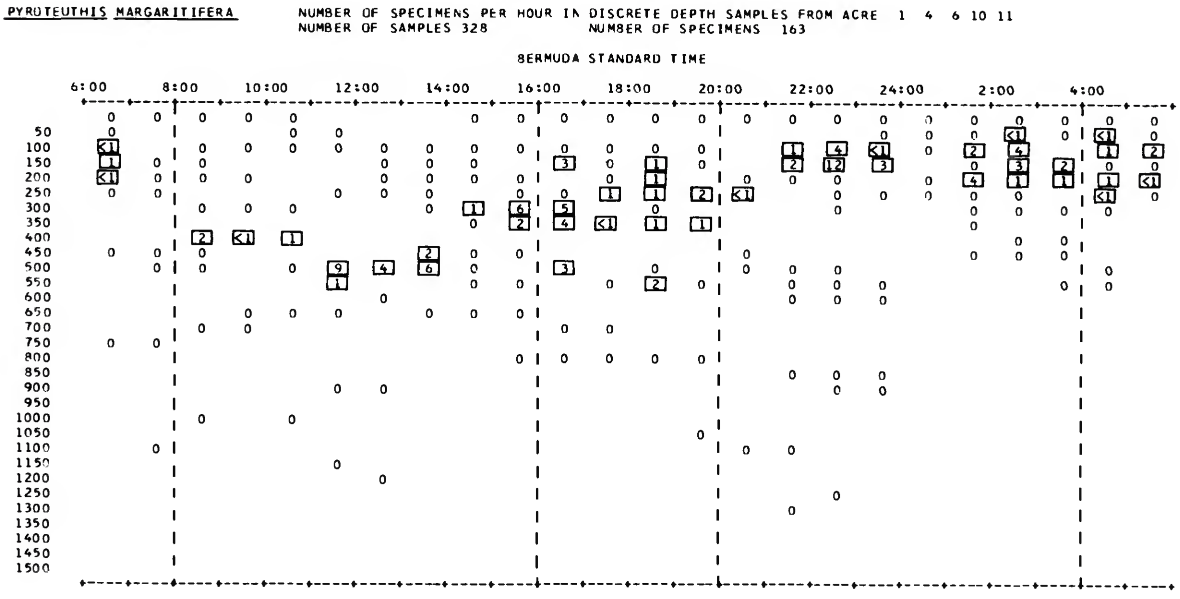

FIGURE 3.—Vertical distribution of *Pyroteuthis margaritifera* off Bermuda. Time-depth plot of positive and negative captures and sampling effort. (See page 11 for explanation of symbols.)

24-hour cycle, as well as the time-depth location of samples that caught no specimens of *P. margaritifera* (indicated by a zero); blank spaces represent time-depth loci that were not sampled. During the day over 80 percent of the 43 specimens captured came from 375–500 m. Sixty-two specimens were captured at night from 75–175 m. *Pyroteuthis margaritifera,* therefore, undergoes a diel vertical migration of about 300–350 m.

During the daytime there is no size stratification with depth. At night a possible size stratification may occur but data are inconclusive. During the day only a single adult was captured while at night three were captured.

In *Pterygioteuthis* 130 specimens of *P. gemmata* from open nets were available for analysis from California after elimination of "larval" specimens less than 11 mm ML and twilight captures (Figure 4). Of the 56 daytime captures, 3 percent were taken in the upper 300 m; 56 percent were taken from 300–600 m; 25 percent from 600–900 m; and 16 percent from 900–1200 m. A small peak is present at 700–800 m as a result of a single trawl which likely captured the specimens during retrieval through the upper layers. The daytime captures predominate between 300 and 600 m, and the catches below 600 m presumably represent contamination.

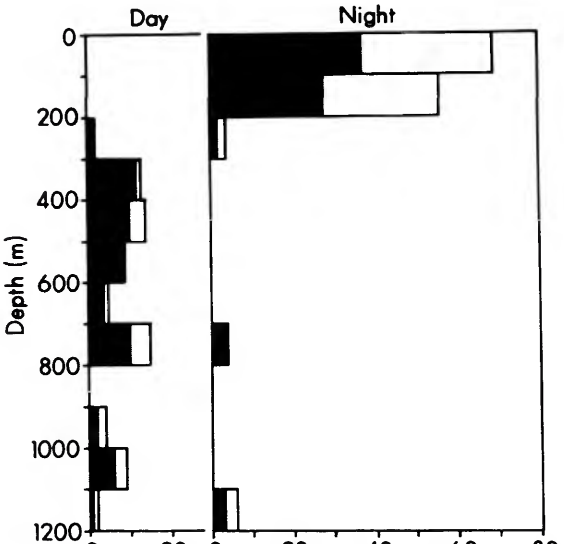

FIGURE 4.—Vertical distribution of *Pterygioteuthis gemmata* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

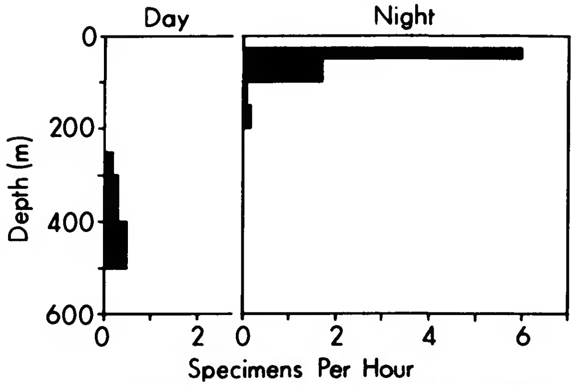

FIGURE 5.—Vertical distribution of *Pterygioteuthis giardi* off Bermuda. (Black bar = number of specimens captured.)

The nighttime distribution shows 88 percent of the 74 specimens in the upper 200 m. The few captures below this level probably are contaminants. *Pterygioteuthis gemmata* from California, therefore, appears to undergo a diel migration of about 300–400 m in vertical extent.

Another species of *Pterygioteuthis, P. giardi,* has been taken during the Ocean Acre cruises off Bermuda. One hundred four specimens of *P. giardi* were captured in closing net samples (Figure 5). During daytime, six specimens (8–16 mm ML) were captured, five from 327–475 m and one at 260 m (9 mm ML). At night 70 specimens (5–16 mm ML) were captured between 50 and 175 m; all but three were captured between 50 and 100 m, and over 80 percent of the captures occurred at 50–60 m. *Pterygioteuthis giardi,* therefore, undergoes a diel vertical excursion of 250–300 m. There is no apparent segregation of sizes during day or nighttime periods.

It is difficult to explain the large disparity between number of individuals captured in day vs night trawls. It is possible that there is an avoidance of the net during the daytime due to the greater light intensities or that the discrepancy reflects a greater dispersion of individuals during the day.

The Ancistrochirinae contains two species, one of which, *Thelidioteuthis alessandrinii,* may be a synonym of the other, *Ancistrochirus lesueuri.*

Four larval and juvenile specimens (15–33 mm ML) of *T. alessandrinii* were captured by the Dana Expeditions on four separate occasions in less than 100 m at night. Two specimens (20 mm and 21 mm ML) were taken at night off Bermuda in closing nets in less than 125 m. One specimen (35 mm ML) was taken in an open net at 80 m at night off Hawaii. The nighttime distribution of juveniles, at least, appears to be in the near-surface layers.

The preceding data on the family Enoploteuthidae demonstrate that several species undergo diel vertical migration of several hundred meters. Where known, all stages beyond the larval stage for a particular species appear to occupy the same depth zones; even individuals as small as 5 mm ML (e.g., *Pyroteuthis margaritifera*) may migrate with adults. While daytime captures are few or lacking for many species, nighttime captures of individuals of many other species in near-surface waters suggest that the migratory behavior demonstrated in a few species probably is very widespread in the family. Indeed, no evidence exists for nonmigratory behavior of any enoploteuthid species.

OMMASTREPHIDAE

FIGURE 26

We have relatively little additional information on the vertical distribution of this large and important family since Clarke (1966) reviewed much of the literature covering the subject.

Ommastrephes caroli, O. pteropus, and *O. bartramii* are frequently dipnetted at the surface at night (Clarke, 1966; Roper, 1963; Young, 1972a). A tentacle of *O. caroli* was caught by a reversing water bottle at 1490 m, presumably during the night, and photographs, apparently of this species, were taken at night at 600 and 700 m (Clarke, 1966:108–109). Little is known about their daytime distribution. Baker (1960) reported that specimens of *O. pteropus* (or *O. caroli*, see Clarke, 1966:109) were photographed and captured on long lines at 1000 m at night at the same time that other individuals of these species were being captured at the surface. These are prominant species at the surface at night except during periods of bright moonlight and rough seas (Baker, 1960). Arata (1954) observed squid, thought to be *O. bartramii*, leaping from the water and gliding for some distance over the water surface during the daytime.

Symplectoteuthis oualaniensis commonly is found at the surface at night (Clarke, 1966:115). *Symplectoteuthis luminosa* has also been reported from the surface at night (Young, 1972a:34). Nothing is known of the daytime distribution of these species.

Hyaloteuthis pelagica, distributed world-wide in warm waters, is a relatively infrequently captured ommastrephid. Off Bermuda, four specimens (12–24 mm ML) have been taken in closing nets at night at 100 m. Open-net captures with a large Engel midwater trawl resulted in the capture of 85 specimens (10–90 mm ML, mostly 40–90 mm ML), 78 of which were taken at night; the remaining 7 were twilight captures. At night 56 specimens were taken at 150–0 m; the remaining 22 specimens taken in trawls fishing at various depths to 1000 m, probably are contaminants.

Dosidicus gigas commonly is seen at the surface at night (Clarke, 1966:117). We have seen motion pictures of this species leaping from the water during the day off Chile and attacking fishing lures at the surface during the day off Peru.

Ornithoteuthis antillarum has been reported at the surface at night (G. L. Voss, 1957). Sasaki (1929:285) reported that *O. volatilis* is referred to as flying squid by Japanese fishermen who report that it can glide over the surface of the sea.

Data are available on 43 adult specimens of *O. antillarum* from the western tropical Atlantic and Caribbean; all captures were made in bottom-fishing otter trawls (21 tows) at depths of 585–1100 m (mostly 640–825 m), and all but three were captured during the day. The three possible nighttime captures were made in nets that fished through twilight periods as well as night. In the eastern south Atlantic, many specimens of *O.* cf. *antillarum* were captured at night over deep water in Engel trawls that fished between 100 and 600 m. The significant preponderance of daytime vs nighttime captures in bottom trawls and the occurrence of specimens in midwater and at the surface at night suggest that *Ornithoteuthis* spends the day on or near the bottom and spreads out into middepths at night.

Illex illecebrosus generally is caught in shallow water 15–30 m deep during the summer. At the northern end of its range, off Newfoundland, these squid are occasionally seen at the surface (C. C. Lu, pers. comm.). Clarke (1966:119) stated that *Illex illecebrosus* is most numerous near the coast and probably lives on the upper slope and shelf.

Illex illecebrosus off the Chesapeake Bight has been captured with otter trawls at depths of 45–265 m; nearly all captures occur during the daytime indicating that specimens leave the bottom and disperse into midwater at night (C. C. Lu, pers. comm.). Milliman and Manheim (1968) observed dense concentrations (estimated to be 500 per 10^3m^3) of squid off Cape Hatteras, North Carolina, thought to be *Illex illecebrosus*, from a submersible at depths of 220–250 m during the day over a bottom depth of 700 m. C. R. Robins (University of Miami, pers. comm.) observed considerable numbers of squid, thought to be a species of *Illex*, from a submersible at approximately 900 m during daytime off Miami, Florida. Some of the squid were resting on the bottom while others were swimming immediately above the bottom.

Illex coindetti is closely associated with the bottom where it is fished at depths of about 40 to 500 m depending somewhat on the locality and season (Mangold-Wirz, 1963:157). In the Gulf of Guinea, *I. coindetii* has been captured in otter trawls from 80–410 m during the daylight hours; at night the specimens apparently leave the bottom and disperse into middepths (C. C. Lu, pers. comm.). *Illex oxygonius* from the western Atlantic has been taken from 50–550 m with bottom trawls (Roper, Lu, and Mangold, 1969:219); no information is available on day-night distributions. *Todaropsis eblanae* also is associated with the bottom and is fished at depths from 85–660 m (Mangold-Wirz, 1963:168).

Todarodes sagittatus frequently is found at the surface during the night, but during the day it can be fished with bottom trawls from 70–800 m (Clarke, 1966:129). It has been photographed at depths of 1000 m presumably far off the bottom (Clarke, 1966:129). Clarke and Merrett (1972) record fragments of *T. sagittatus* from the stomach of the bottom-living shark, *Centroscymnus coelolepis*, captured at 1975 m.

Todarodes pacificus commonly is caught by jig and line at 20–30 m from the surface at night. During the day these squid descend to around 100 m where they are occasionally fished by hand line (Suzuki, 1963:143).

Little information is available on the vertical distribution of species of the genus *Nototodarus*. *Nototodarus sloani gouldi* has been taken by dipnets (Cotton, 1942). In Hawaii, *N. hawaiiensis* appears to be associated with the ocean bottom as evidenced by occasional bottom photographs (400 m by R. Grigg, University of Hawaii), otter trawl captures (400–570 m, ALBATROSS stations, vide Berry, 1914), and trap captures. During late summer months it can be captured at the surface at night off the island of Hawaii where it supports a minor dipnet fishery.

The ommastrephids exhibit a wide variety of vertical distributional patterns. Some species (e.g., *Ommastrephes caroli*) can roam from the surface to great depths. Others appear to be restricted to near surface waters (e.g., *T. pacificus*). A number of species are associated with the bottom, but approach the surface nightly during all or part of the year (e.g., *T. sagittatus, N. hawaiiensis*). Other species may move into shallow water seasonally during feeding migrations (e.g., *I. illecebrosus*).

HISTIOTEUTHIDAE

FIGURES 6, 27: BARS 1–4

The Histioteuthidae consists of 13 species in the single genus *Histioteuthis* (N. Voss, 1969). Since most species are represented by relatively few specimens captured in open nets from scattered localities, information on vertical distribution is sketchy.

Histioteuthis heteropsis from the California study is represented by 191 specimens larger than 6 mm ML taken in open nets (Figure 6). During the daytime 90 specimens were taken, none of which occurred in the upper 300 m; 3 percent were taken in 300–400 m, 13 percent in 400–500 m, 38 percent in 500–600 m, 24 percent in 600–700 m, and 10 percent in 700–800 m. The remaining 12 percent were scattered between 800 and 1200 m and probably represent contamination. The upper limit for the majority of the daytime captures is 400 m and the lower limit lies around 800 m. Peak abundance occurs between 500 m and 700 m.

At nighttime 69 percent of the 101 specimens

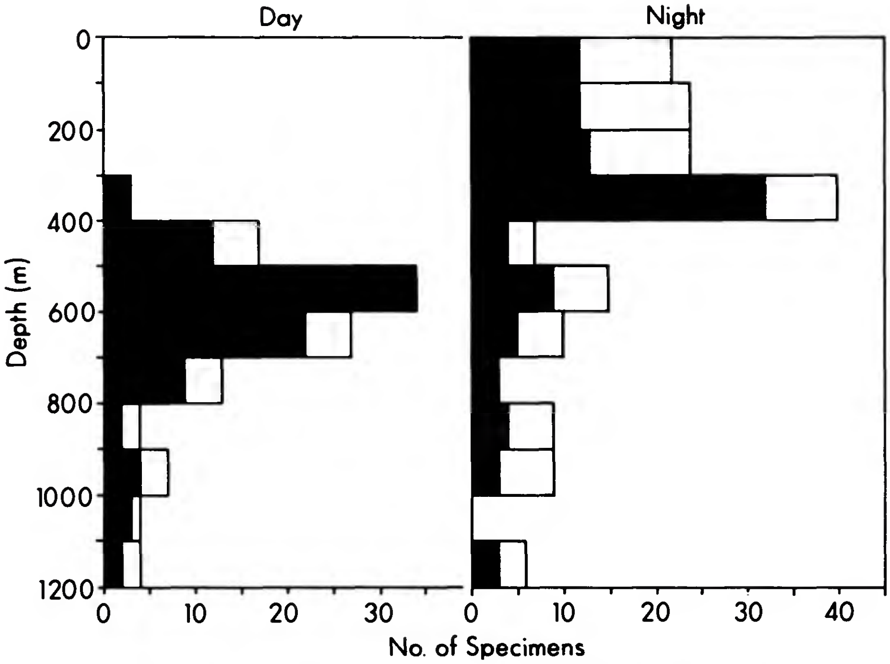

FIGURE 6.—Vertical distribution of *Histioteuthis heteropsis* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

captured were taken in the upper 400 m with a peak at 300–400 meters; 21 percent from 400–800 m, and 10 percent from 800–1200 m. Possibly all specimens from below 400 m are contaminants. The shallowest capture at night for specimens larger than 20 mm ML was 200 m and most were concentrated at 300–400 m. This species undergoes a diel vertical migration of 300 to 400 m.

From off Bermuda closing net captures of *H. dofleini* were made during the day at 510 m (14 mm ML) and at night at 50 m (12 mm ML). One *H. meleagroteuthis* (16 mm ML) was captured at 690 m during the day and another (32 mm ML) was taken at 360 m at night. Two specimens of *H. corona* (25 mm and 27 mm ML) were captured during the day at 630 m. We suspect that a diel vertical migration pattern probably is widespread in this family.

PSYCHROTEUTHIDAE

The family consists of a single genus, *Psychroteuthis*, which contains two species (one undescribed) that occur in Antarctic waters and, possibly, a third species from off the Bonin Islands (Roper and Young, 1972:220). A large specimen was taken through an ice hole in the Antarctic and other specimens are known from midwater trawl captures. Nothing definitive, however, is known of the vertical distribution of these species.

NEOTEUTHIDAE

FIGURE 29: BAR 1

Two genera are known in the Neoteuthidae, *Neoteuthis* and *Alluroteuthis*. *Alluroteuthis antarcticus* is a pelagic species abundant in Antarctic waters, but little information currently is available on its vertical distribution.

Neoteuthis thielei is known from only a few specimens that have been captured in open midwater trawls. Off California one specimen (83 mm ML) was taken at 1333–0 m. In the eastern tropical Atlantic eight specimens (ca. 36–125 mm ML) of *Neoteuthis* sp. were taken at night in open

Engel trawls that fished at 1750–2000 m; one specimen (ca. 130 mm ML) was taken at 1300–0 m at night. In the Gulf of Mexico a specimen (ca. 50 mm ML) was taken at night at 900 m in a closing net.

ARCHITEUTHIDAE

The Architeuthidae consists of 20 nominal species of *Architeuthis*, most of which are undoubtedly synonymous. Although the giant squid has received a great deal of attention in the literature, very little is known of its vertical distribution or of any other aspect of its biology. Occasionally *Architeuthis* has been sighted (F. A. Aldrich, Memorial University of Newfoundland, pers. comm.) or captured alive at or near the surface (Verrill, 1882a:181), but these sightings may be unrepresentative of its habitat. The great majority of specimens come from strandings or whale stomachs. Perhaps the most significant capture is that reported by Cadenat (1936) of a specimen taken in a bottom trawl that fished at about 200 m. Clarke and Merrett (1972) record fragments of *Architeuthis* sp. from the stomach of the deep-sea shark, *Centroscymnus coelolepis*, which was captured on a bottom-set long line at 1246 m.

Two juvenile specimens of *Architeuthis* were taken from stomach contents of the oceanic fish *Alepisaurus ferox* (Roper and Young, 1972); this fish is thought to hunt primarily in the upper 300 m of the open ocean (Rancurel, 1970:82), so it seems probable that the young *Architeuthis* occur within this range.

BATHYTEUTHIDAE

FIGURES 7, 27: BARS 5–7

The Bathyteuthidae consists of three species in the genus *Bathyteuthis*. Details of the distribution of these bathypelagic species are reported by Roper (1969).

Bathyteuthis abyssicola is a very commonly caught species in Antarctic waters and it occurs less abundantly in other areas of the world ocean; its maximum distribution appears to be directly associated with areas of relatively high organic productivity at the surface of the sea and with waters of 1°–5° C. In the Antarctic 563 specimens were analyzed (Figure 7). All specimens were captured in open net trawls; 87 percent of the captures occurred between 1000 and 2500 m, and the remainder were taken between 500 and 1000 m. A very few captures occurred below 2500 m and are considered to be contaminants. Of the total captures, 60 percent (340 specimens) occur between 1500 and 2500 m.

No diel vertical movements are known to occur. Larger animals tend to occur at greater depths than smaller individuals. Sixty-one percent of the specimens less than 300 mm ML live between 500–1500 m, while 72.5 percent of those larger than 30 mm ML live between 1500–2500 m.

One specimen of *B. abyssicola* (30 mm ML)

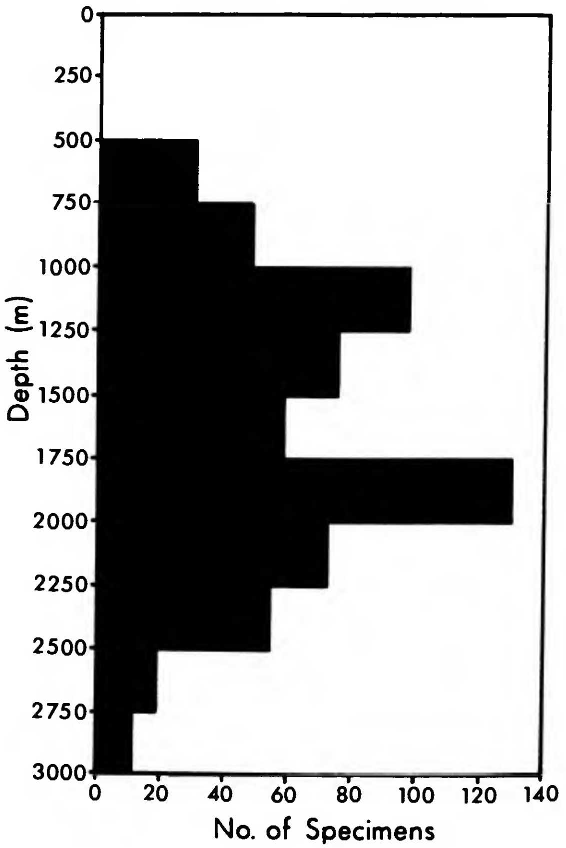

FIGURE 7.—Vertical distribution of *Bathyteuthis abyssicola* from Antarctic waters. (Black bar = number of specimens per standardized 2-hour tow.)

was captured in a closing net that fished between 830 and 975 m during the day off Hawaii.

Bathyteuthis bacidifera has been taken between 680 and 1550 m from the tropical eastern Pacific in open nets. *Bathyteuthis berryi* from off California has been captured between 800 and 1200 m in open nets and probably occurs much deeper, but data on deep water captures are lacking.

GONATIDAE

Figures 8–12, 27: bars 8–14

Members of the Gonatidae inhabit primarily high latitude waters (Nesis, 1971a). Three genera presently are known; *Gonatus, Gonatopsis,* and *Berryteuthis,* although recent work has made the generic boundaries uncertain (Okiyama, 1969; Fields and Gauley, 1971; Nesis, 1971b).

Gonatus onyx was the most abundant species taken in the California study. Seven hundred and seventy-four specimens over 21 mm ML from open trawls were used in determining patterns of vertical distribution (Figure 8).

Less than 2 percent of the 438 daytime captures were shallower than 400 m; 87 percent of the specimens were taken in a zone between 400 and 800 m. Specimens captured below 800 m are probably contaminants.

At night 3 percent of the 336 specimens were taken in the upper 100 m; 11 percent in 100–200 m, 5 percent in 200–300 m, 18 percent in 300–400 m, and 48 percent in 400–500 m. The remaining 12 percent below 500 m probably represent contamination. Thirty-seven percent of the nighttime captures were taken from the water above the upper limit of the daytime captures (400 m), and the lower limit of the nighttime distribution appears to be 300 m shallower than the lower limit of the daytime distribution.

This species apparently shifts upward at night primarily into the 300–500 m zone, but ranges into the upper 100 m. Trawls that caught *Gonatus onyx* during the day between 400 and 800 m averaged 16.8 specimens per tow. At nighttime between 300 and 500 m the average catch was 16.0, while between 0 and 300 m the average was only 4.0.

Gonatus californiensis was the least abundant member of the genus in the California study. Of the 99 specimens larger than 20 mm ML, 46 were twilight captures unsuitable for plotting diel ver-

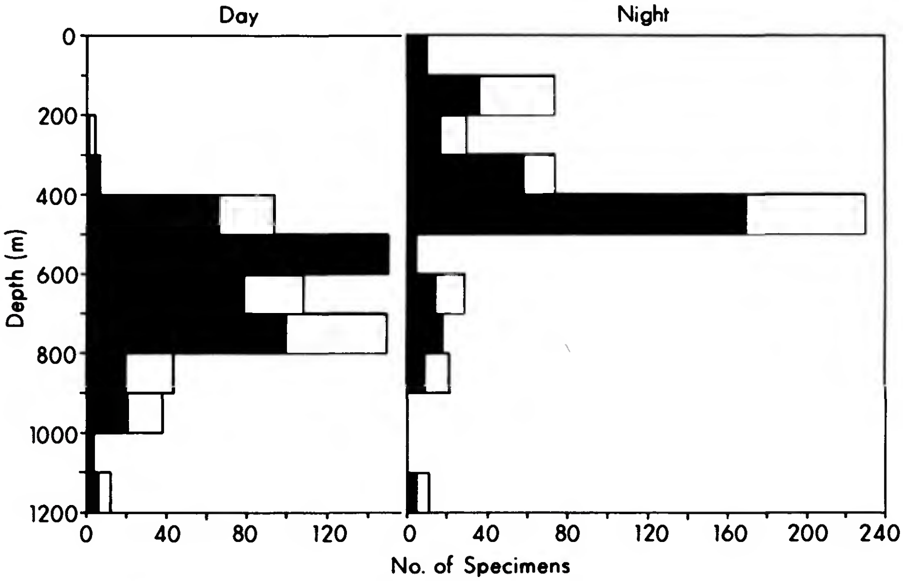

Figure 8.—Vertical distribution of *Gonatus onyx* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

tical distribution. The data are difficult to interpret and for this reason the figure showing total captures (day, night, twilight) is included with the day and night distribution figures (Figure 9). During the daytime no specimens were captured above 400 m. Seventy percent of the 30 daytime captures were taken in the zone from 400–800 m with the greatest proportion, 30 percent, occurring at the 700–800 m level. The remaining 30 percent is scattered from 800–1200 m and may represent contamination. Even though the daylight captures are few, the upper and lower limits of the daytime distribution appear to be at 400 and 800 m, respectively, if twilight captures are considered. Eighty-eight percent of the combined daytime and twilight captures occurred between 400 and 800 m.

Only 23 specimens were suitable for the nighttime analysis. Thirty-five percent were taken from 100–400 m and 61 percent from 400–800 m; a slight peak (48 percent of the night specimens) occurs between 300 and 500 m. While the number of specimens is inadequate to allow definite conclusions, this species seems to undergo an upward shift at night.

Eighty-eight specimens of *Gonatus pyros* over 20 mm ML are available from the California study (Figure 10). Only a single specimen was captured above 400 m during the daytime; 86 percent of the 52 daytime captures were taken in a zone between 400–700 m. The few specimens captured below 700 m probably are contaminants. The daytime distribution of this species appears to be between 400 m and 700 m.

Thirty-six specimens were taken during the nighttime; 14 percent in 100–200 m, 6 percent in 200–300 m, 42 percent in 300–400 m, and 17 per-

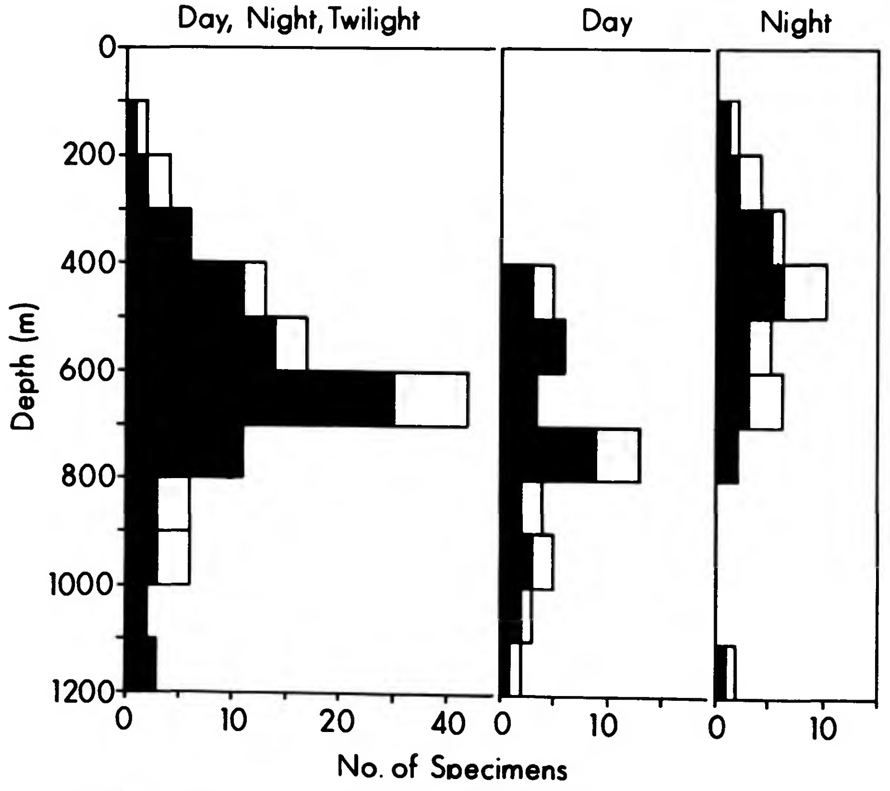

FIGURE 9.—Vertical distribution of *Gonatus californiensis* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

cent in 400–500 m. The remaining 21 percent of the specimens below 500 m possibly are contaminants. Therefore, the limited data suggest that the nighttime distribution has an upper limit at 100 m and a lower limit at 500 m, although most captures were at 300–400 m; this indicates that the species shifts upward at night.

Eighty-seven specimens of *Gonatus berryi* from off California were suitable for plotting vertical distribution. Although fairly common, this species is never caught in large numbers. The larvae of *G. berryi* differ morphologically from the larvae of the other three species of *Gonatus* in the area studied, and this is reflected in their deeper living habit. The distribution of larvae (6–15 mm ML) shows a peak between 300 and 700 m (Figure 11). This range is slightly shallower than that found for the larger animals.

No subadult specimens were captured in less than 300 m during the daytime. A single specimen each was captured in the 300–400 m zone and the 400–500 m zone; 68 percent of the catch was in the 500–800 m zone, while the remaining specimens below 800 m probably represent contamination. Therefore, the daytime distribution seems to lie between 500 and 800 m. A large number of captures in the 400–500 m zone was made in tows that extended into the twilight period; many of these probably entered the net during daytime, so the upper limit may be at 400 m instead of 500 m.

At nighttime no specimens were taken in the upper 100 m; one was taken in 100–200 m, three in 200–300 m, and one in 300–400 m. The greatest concentration is in the 400–500 m zone where 33 percent of the specimens were taken, while 30 percent were taken between 500–800 m. While there might be a slight upward shift in the peak of abundance at night, it is not as apparent as in the other species of *Gonatus*. The number of captures attributed to depths below 800 m during both daytime and nighttime is considerably higher than is found in the other three species of *Gonatus*. Although much of this undoubtedly is contamination, a small percentage of the population probably extends to the lower limit (1200 m) of the sampling program. Church (1971) observed a specimen of *Gonatus*, apparently *berryi*, from a deep-diving submersible at 915 m.

Gonatopsis borealis from off California was represented by 74 juvenile specimens between 16 and 47 mm ML (Figure 12). No specimens were captured during the daytime in the upper 300 m and only a single specimen was taken in the 300–400 m zone. Ninety percent of the daytime captures occurred at 400–700 m, while 8 percent, probably contaminants, were captured below 700 m. Therefore, the distribution in the daytime seems to be between 400 and 700 m.

Only a few specimens were captured at night; three in the upper 200 m, six in 200–400 m, one in 400–500 m, and three, probably contaminants, in 800–1000 m. The scanty evidence suggests that the nighttime distribution is in the upper 400 m. If this is correct, *G. borealis* undergoes vertical migration of 200–300 m, at least during the juvenile stage.

Fourteen specimens of *Berryteuthis magister* are available from the Auke Bay region of Alaska. Some specimens were captured in otter trawls at depths that ranged from 165–310 m during both day and night. The specimens had the following mantle lengths (in mm): 69, 73, 100, 152, 192, 200, 210, 250. Three specimens (57, 75, and 90 mm

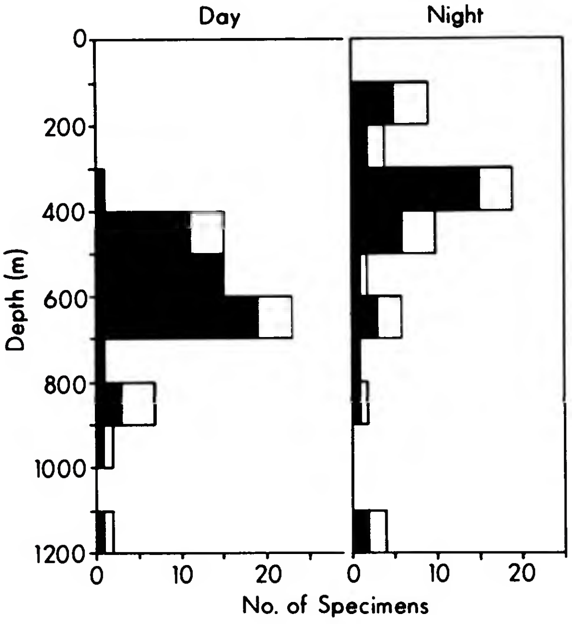

FIGURE 10.—Vertical distribution of *Gonatus pyros* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

ML) were taken in Isaacs-Kidd midwater trawls at night between 3–5 m, and 3 others (62, 124, and 173 mm ML) were taken at or near the surface in a herring seine and salmon traps. Sasaki (1929:272) records *B. magister* from 180, 725, 820, and 1000 m, in bottom trawls off Japan, Korea, and the Bering Sea.

Berryteuthis anonychus has been recorded (as *Gonatus anonychus*) only from specimens that were captured at the surface at night off Oregon (Pearcy and Voss, 1963).

Three of the four species of *Gonatus* (*G. pyros, G. onyx, G. californiensis*) for which we have data, exhibit very similar distributional patterns, in which they appear to undergo a slight upward shift in their vertical distributions at night. The absence of strong vertical migrations in these species is somewhat surprising, because they are among the more muscular midwater squids. It is possible that the fourth species (*G. berryi*) does not migrate vertically. Juvenile *Gonatopsis berryi* seem to exhibit a more pronounced upward shift, but nighttime data are insufficient to confirm this.

Berryteuthis magister has been taken many times in bottom trawls and probably spends some time associated with the ocean bottom.

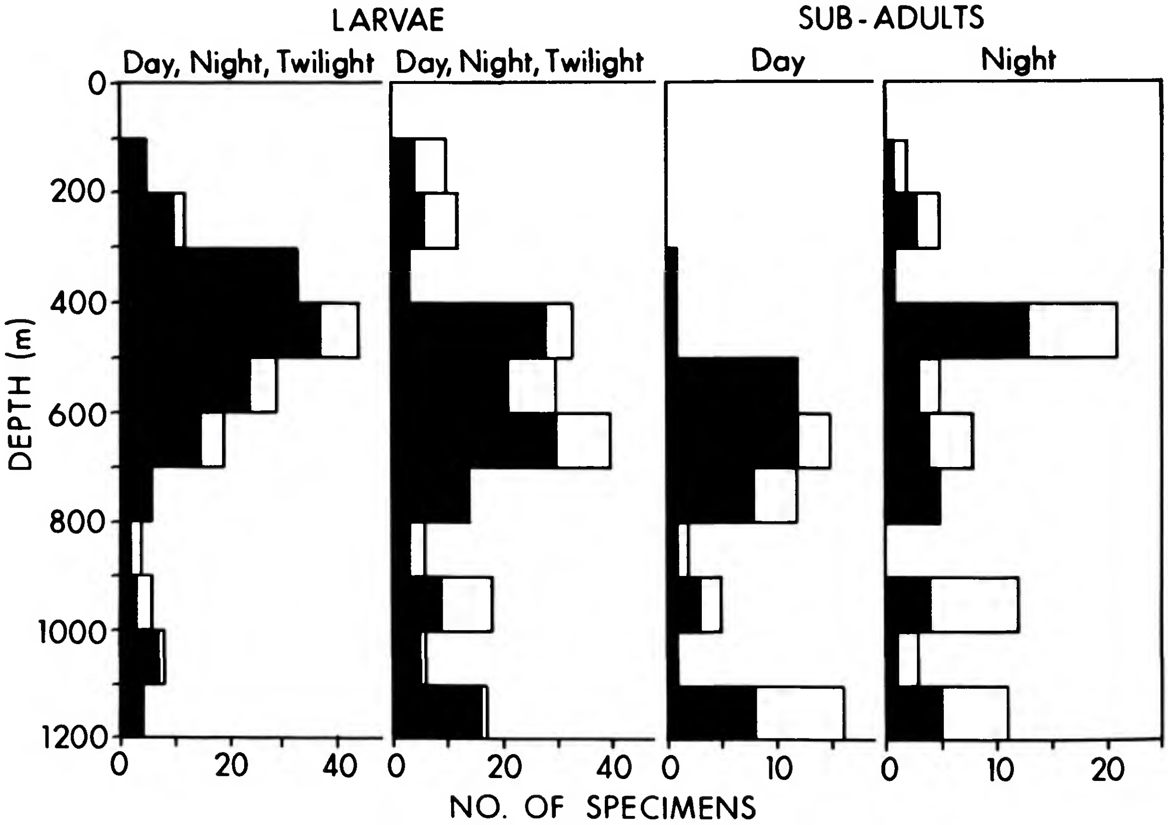

FIGURE 11.—Vertical distribution of *Gonatus berryi* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

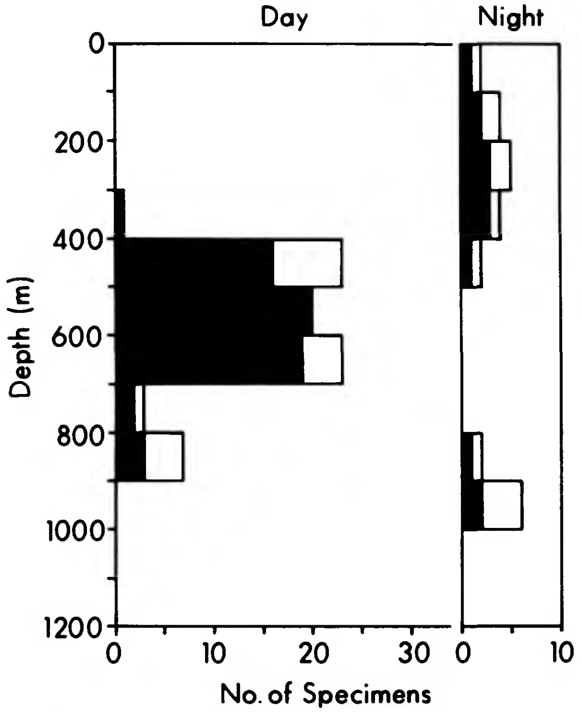

FIGURE 12.—Vertical distribution of *Gonatopsis borealis* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

OCTOPOTEUTHIDAE

FIGURES 13, 28: BARS 5, 6

The Octopoteuthidae consists of two genera, *Octopoteuthis* and *Taningia.*

Eighty-three specimens larger than 15 mm ML of *Octopoteuthis deletron* from California were analyzed (Figures 13, 28:bar 5). Only about half as many specimens (26) were captured during the daytime as at night. During the day, no specimens were captured in the upper 200 m. The greatest number of captures occurs between 300 and 400 m where 13 specimens (50 percent) were taken (when the amount of trawling at different depths is equalized, the greatest abundance would be at 200–300 m). Three specimens each were taken in 400–500 m, 500–600 m, and 600–700 m; a single specimen was taken in 700–800 m, and three between 1000 and 1200 m. The daytime upper limit is clearly at 200 m, but the lower limit is more difficult to determine.

Fifty-seven specimens were captured at night, the majority of which were fairly evenly distributed throughout the upper 500 m; 23 percent in the upper 100 m, 14 percent in 100–200 m, 11 percent in 200–300 m, 21 percent in 300–400 m, and 12 percent in 400–500 m. The remaining 19 percent was distributed from 600–1200 m and probably represents contamination from shallower zones.

Certainly additional information is needed, but the available data indicate that the species does not undergo a "typical" diel vertical migration, but seems to spread out over a greater range of depths during the night than during the day.

The largest *Octopoteuthis* (20 mm ML) taken off Bermuda in closing nets was captured at 230 m at night.

Little information exists on *Taningia danae,* the only species in the genus. *Taningia danae* grows to a large size of at least 140 cm ML (Clarke, 1967, table 1). A few juveniles have been captured at night within 175 m of the surface (Clarke, 1967: 127). Remains of a large *T. danae,* estimated to approach 50 kg, were taken from the stomach of the bottom-living shark, *Centroscymnus coelolepis,*

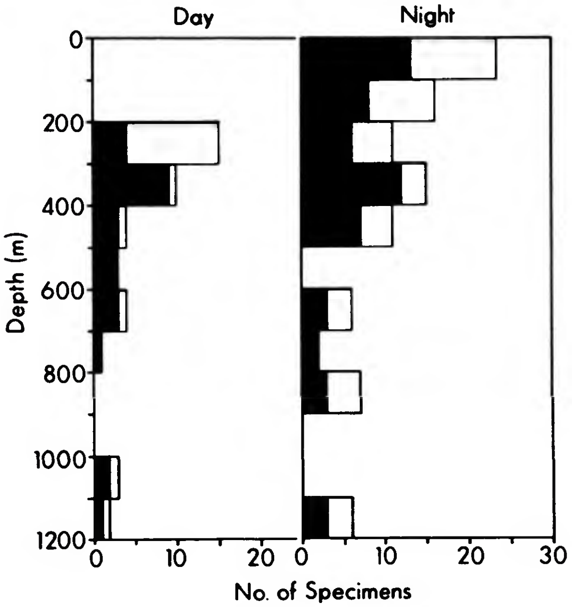

FIGURE 13.—Vertical distribution of *Octopoteuthis deletron* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

captured on a bottom-set long line at 1246 m (Clarke and Merrett, 1972). Otherwise, nothing definitive is known of the distribution of the larger animals.

ONYCHOTEUTHIDAE

FIGURE 28: BARS 2–4

The family Onychoteuthidae contains five genera, the best known of which is *Onychoteuthis. Onychoteuthis banksii* occasionally is found on the decks of ships in the morning (Rees, 1949) and individuals are frequently observed and dip-netted at the surface at night (personal observations). The animals are powerful swimmers and adults only rarely are caught in nets.

Off Bermuda, 52 specimens of *Onychoteuthis banksii* (5–57 mm ML) were taken in closing net samples. Captures were made from the surface to a maximum depth of 150 m; all but two specimens were taken in the 50–100 m zone both day and night. The largest specimen was taken at the surface at night. All daytime captures from Ocean Acre are small individuals which may not have adopted the juvenile or adult pattern of distribution; thus little can be determined concerning daytime distribution. However, a specimen of 20 mm ML was taken from a depth of 800 m in midday in the Mediterranean in a closing trawl. Although it is possible that this was a contaminant, examination of the photosensitive vesicles of *Onychoteuthis*, which are rather elaborate, suggests that this animal is not restricted to epipelagic regions.

Onykia caribaea is a relatively small species that has been taken primarily at the surface both during the day and at night. It is commonly associated with *Sargassum*, the floating seaweed (Lesueur, 1821; Bullen, 1899; personal observations). *Onykia caribaea* has a bluish coloration on the dorsal surface that is characteristic of species of the neuston (Herring, 1967:220). One specimen of *O. caribaea* (34 mm ML) from St. Helena was regurgitated from the stomach of a Fairy tern which feeds only at the surface.

Ten closing net captures of juvenile *O. caribaea* have been made during the Ocean Acre cruises and all specimens were taken at the surface both during the day and at night.

Chaunoteuthis mollis is known from only a few specimens, several of which were taken dead at the surface (Clarke, 1966:149).

The vertical distribution of *Ancistroteuthis lichtensteini*, a rarely caught species, cannot be determined on the basis of the scant information available.

Several nominal species of *Moroteuthis* exist, the best known of which is *M. robusta* from the north Pacific. Records are available from the bottom trawl fisheries off the west coast of North America from central California to Vancouver. Specimens recorded in the literature have been taken in otter trawls that fished at the following depths (in meters): 165–275, 250–280, 295, 320, 340 (2 stations), 350, 370 (3 stations), 400 (2 stations), 460, and 550 (Pattie, 1968; van Hyning and Magill, 1964; Smith, 1963). One specimen was captured by skin divers in shallow water in central California, which presumably is an abnormally shallow occurrence for this species, since the shallow water fisheries have failed to yield additional shallow water records.

R. R. Talmadge (pers. comm.), utilizing information and specimens provided by sole fishermen, reports that a specimen of *M. robusta* was captured at 100 m and that specimens are commonly captured from 200–275 m on down to 375 m. The currently known distribution may well be incomplete, in that it reflects only the depths at which fishermen concentrate their fishing efforts for various species of sole. Fishermen report that *M. robusta* may be caught both during day and night, and that no correlation between depth of capture and time of day seems to exist. Although most captures occur in the fall (August to November), specimens may be caught throughout the year. Occurrence in northern Californian waters appears to be cyclic and the species may be absent one year and abundant the next.

Currently, sufficient data are lacking to indicate the deeper boundary of *M. robusta*, although the upper limit appears to be around 100 m. Since all captures have been made by bottom trawls, it is probable that this species is associated with the bottom, at least part of the time. Furthermore, about half of the specimens examined by Talmadge (pers. comm.) contained in their stomachs fragments of the sea urchin, *Briaster townsendii* which lives on mud bottom from about 275 m to 900 m.

In summary, little can be said about the vertical distribution of most species of onychoteuthids. It is clear that *Onychoteuthis banksii* occurs in surface waters at night. *Onykia caribaea* apparently is restricted to surface waters both during the day and night. As with many ommastrephids and loliginids, *Moroteuthis robusta* seems to associate with the ocean bottom at least part of the time. Almost no information is available on the distribution of *Chaunoteuthis* and *Ancistroteuthis*.

THYSANOTEUTHIDAE

FIGURE 28: BAR 1

Thysanoteuthis rhombus is a world-wide oceanic species in lower latitudes. In the Japan Sea it is taken in set nets during the fall and early winter in near-shore waters (Nishimura, 1966:329); it is caught in greater abundance during the night but daytime captures are relatively common. We have a juvenile specimen of *T. rhombus* (25 mm ML) that was captured in the open ocean (bottom depth 2750 m) in an open midwater trawl that fished during the day at 35–55 m.

CYCLOTEUTHIDAE

FIGURE 28: BARS 7–9

This family contains three (possibly four) species in two genera, *Cycloteuthis* and *Discoteuthis*; each species is known from only a few specimens. Five specimens of *Cycloteuthis sirventi* (17–134 mm ML) have been caught at 650–0 m during the day; 140–0 m, 150–0 m, and 100–0 m at night and 200–0 m at twilight in open nets. Five specimens of *Discoteuthis discus* (24–53 mm ML), were captured at 750–0 m and 450–0 m during the day; 400–0 and 100–0 m at night, and 600–0 m (time unknown). These records have been taken from scattered localities throughout the north Atlantic (Young and Roper, 1969a). Two adults have been taken off Bermuda in open nets at depths of 140–0 m and 950–0 m, at night.

Discoteuthis laciniosa (19–134 mm ML) has been taken in open nets that fished at 425–0 m, 725–0 m, 950–0 m, and 1060–0 m during the day and at 160–0 m, 350–0 m, 500–0 m, 750–0 m (2 specimens) and 1200–0 m at night. *D. laciniosa* has been taken off Hawaii in open nets at 900–0 m during the day (55 mm ML) and 215–0 m at night (40 mm and 50 mm ML). Several specimens were recently captured in a closing net at 650 m during the day.

With broad scatter of depth-points for the cycloteuthid species, little can be said about their vertical distributions; however, all three species have been captured in the upper 200 m at night.

CTENOPTERYGIDAE

FIGURE 28: BAR 10

The single genus, *Ctenopteryx*, is comprised of several nominal species. Little is known concerning their vertical distribution. From the Mediterranean two specimens (19 and 35 mm ML) of *C. sicula* were captured in closing nets at night between 100 and 150 m. Off Bermuda a single specimen of *C. sicula* (22 mm ML) was taken at 100 m at night in a closing net. Off Hawaii four specimens of *Ctenopteryx* sp. (23–35 mm ML) have been taken at night from 100–0 m. These species appear to inhabit the near-surface waters at night.

During the day only three closing net records are available. Off Bermuda two specimens (12 and 14 mm ML) were caught at 350 m. In the Mediterranean one specimen (12 mm ML) was taken at 150 m. Off Hawaii five specimens (20–29 mm ML) have been taken in open nets between 600–0 m and 800–0 m during the day.

In the Atlantic Ocean in open nets three specimens (38–62 mm ML) were taken at 850–0 m and 1000–0 m during the day; at night 10 specimens (20–58 mm ML) were taken at 100–300 m, five specimens (20–77 mm ML) at 600–800 m, and five specimens (42–83 mm ML) at 1300–2000 m.

BRACHIOTEUTHIDAE

FIGURE 29: BAR 2

The family contains a single genus and an indeterminate number of species. Very little is known of the vertical distribution of any species.

Two specimens of *Brachioteuthis* sp. were taken in closing nets off Hawaii, one at 830–975 m during the day (38 mm ML) and one at 100–150 m at night. Open net captures of four specimens were taken at 975–1000 m during the day (38 mm and 42 mm ML) and at 50 m and 225 m during the night (33 mm and 47 mm ML). In the Mediterranean three specimens (34–63 mm ML) of *Brachioteuthis* sp. were captured in closing nets at 150 m during the night. The meager data suggest that *Brachioteuthis* spp. undergo extensive diel vertical migration.

LEPIDOTEUTHIDAE

FIGURE 28: BARS 11–13

The family tentatively consists of the genera *Lepidoteuthis, Pholidoteuthis,* and *Tetronychoteuthis*. Few reliable records of vertical distribution are available for these genera.

Two juvenile *Lepidoteuthis grimaldii* (60 and 84 mm ML) have been taken at night in open midwater trawls that fished from 270–0 m (Clarke, 1964). A specimen (190 mm ML) was taken in an Engel trawl at 700–0 m at night in the south Atlantic. Off Bermuda one juvenile (35 mm ML) was captured in a closing net at 50 m at night; a second specimen (41 mm ML) was taken in an open net at 585–0 m during the day. All other large specimens available have been taken from the stomachs of large fishes and sperm whales (Clarke, 1966:214), so we have little precise information concerning their vertical distribution.

Three specimens of *Tetronychoteuthis dussumieri* were captured off Bermuda; one (21 mm ML) in a closing net at 350 m during the day, two (44 mm and 100 mm ML) in Engel trawls at night at 1000–0 and 100–0 m, respectively. In the eastern Atlantic seven specimens (36–166 mm ML) were captured in Engel trawls at night at 100–325 m, four (31–159 mm ML) were taken at 600–800 m and one (64 mm ML) at 1800–0 m.

Sixteen specimens of *Pholidoteuthis adami* (all greater than 250 mm ML) are available from the Gulf of Mexico, Caribbean Sea, and northeastern South American waters. All captures were made during the day in bottom trawls from 360–925 m (greatest number of captures 625–750 m). No nighttime trawl captures are known so possibly this species leaves the near-bottom waters and disperses into middepths at night. Voss (1956:132) records the species from 85–870 m in the Gulf of Mexico; all captures were made with bottom trawls. Remains of *P. boschmai* were taken from stomachs of the shark *Centroscymnus coelolepis* captured on bottom-set long lines set at 998–1102 m, 1246 m, 1259 m, 1260 m, and 1472 m (Clarke and Merrett, 1972).

JOUBINITEUTHIDAE

FIGURE 27: BAR 15

The Joubiniteuthidae consists only of *Joubiniteuthis portieri* which is known from a few specimens. Captures were made in open nets that fished at 800–900 m and 2500 m during the day; 2000 m at night; and at 330 m, 350 m, 500 m, and 3500 m at unknown times, although the first three are probably night captures (Young and Roper, 1969b). A large specimen was taken at night in an Engel trawl in the South Atlantic at 1900–0 m.

CHIROTEUTHIDAE

FIGURES 14–16, 29: BARS 3–7

The Chiroteuthidae consists of three genera; *Chiroteuthis, Chiropsis,* and *Valbyteuthis*. Information on the vertical distribution of some species of *Chiroteuthis* and *Valbyteuthis* is available, but the distribution of the monotypic *Chiropsis* is unknown, since only a single specimen of *C. mega* has been taken.

Members of the Chiroteuthidae generally have very distinctive larval stages that may attain a relatively large size before metamorphosis.

Larvae of *Chiroteuthis calyx* compose the bulk of the 136 specimens of this species captured off California. Metamorphosis to the subadult stage takes place when the larva attains a mantle length of 50–60 mm. The vertical distribution of the larvae (Figure 14) presented here is based almost exclusively on specimens larger than 20 mm ML. Generally the youngest specimens live in the upper 100 m, and as they grow they gradually descend to greater depths. In the upper 100 m larvae in the 20–30 mm ML size category are most abundant. At 300–400 m the 30–50 mm ML size range predominates, while at 500–700 m the 40–60 mm ML size category predominates. Specimens taken below 700 m probably are contaminants.

The day-night distribution seems to indicate some larval vertical migration. Specimens were captured in the upper 100 m only at night. In successive (deeper) depth zones, the larger-sized specimens were captured predominantly at night and smaller specimens during the day. This indicates that at night, specimens probably shift upward from their slightly deeper daytime levels.

The subadult population (Figure 15) appears to occupy a zone between 500 m and 800 m during the daytime. Within this zone 14 specimens were captured; no subadults were taken above 500 m. Two additional specimens, probably contaminants, were taken between 1000 m and 1100 m. The 500–800 m zone is approximately the level at which the largest larvae are found.

The vertical distribution of the nighttime population of subadult *C. calyx* is uncertain since only four specimens were captured. One specimen each was captured in 0–100 m, 200–300 m, 300–400 m, and 400–500 m. These captures occurred above the level of the daytime population. The

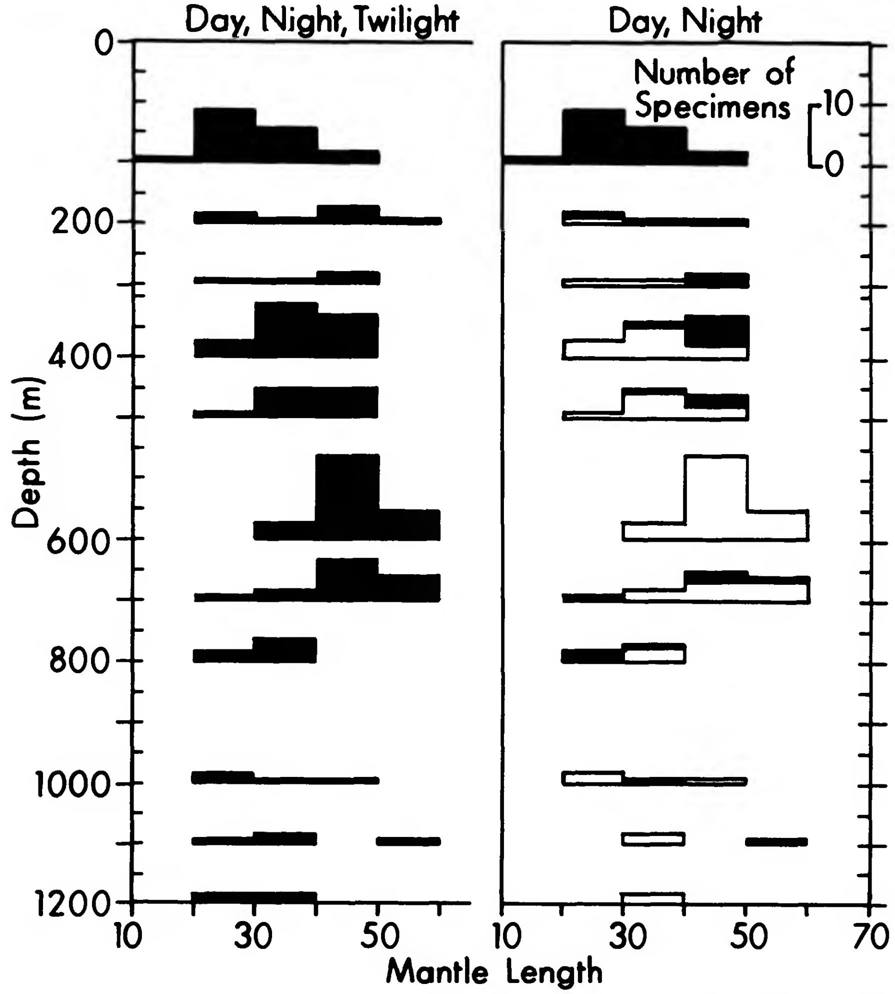

FIGURE 14.—Vertical distribution of the larvae of *Chiroteuthis calyx* off southern California. (Day, Night, Twilight: black bar = total captures; Day, Night: black bar = night captures, white bar = day captures.)

scanty data indicate that a migration or spreading out may occur at night. This interpretation is supported by a few captures from other areas.

Nighttime captures of two subadult *Chiroteuthis* sp. at 167–0 m were made off Bermuda and one subadult *Chiroteuthis* sp. was captured at 150–0 m off Hawaii. One subadult *C. veranyi* was taken in a closing trawl in the Mediterranean at 400 m at night. Three larval *Chiroteuthis* sp. (40–45 mm ML) were captured in a closing net during the day off Hawaii between 600 m and 660 m.

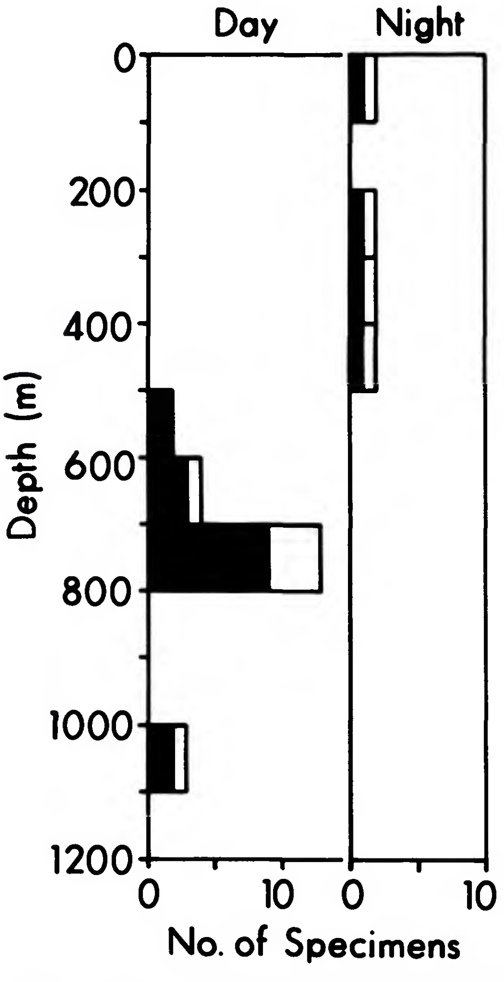

FIGURE 15.—Vertical distribution of subadults of *Chiroteuthis calyx* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

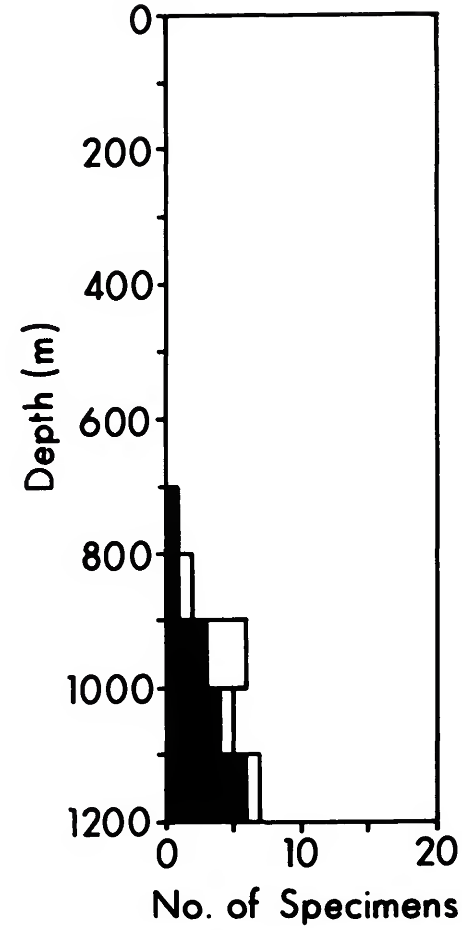

FIGURE 16.—Vertical distribution of *Valbyteuthis oligobessa* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

The records for other species of *Chiroteuthis* are too few and too inconclusive to provide information on their vertical distributions.

Eighteen specimens of *Valbyteuthis oligobessa* were taken off California in 15 different open net tows (Figure 16). No specimens were taken in the upper 700 m. A single specimen was taken at 700–800 m, one at 800–900 m, three at 900–1000 m, four at 1000–1100 m, and six at 1100–1200 m. The shallowest capture is the smallest specimen (23 mm ML). The lower limit of distribution undoubtedly lies deeper than 1200 m, beyond the range of the sampling program. *Valbyteuthis* is one of the deepest living cephalopods taken off California. There is no difference between daytime and nighttime distributions.

Data available on several other species of *Valbyteuthis* also indicate a deep-living habit (Roper and Young, 1967). Specimens larger than 20 mm ML were taken in open nets that fished at (in meters): 530, 683, 1000, 1162, 1250 (2 stations), 1500 (3 stations), 1830, and 2635. Two specimens (35 mm and 50 mm ML) were taken in closing nets off Hawaii at 875–1220 m during the day and 780–955 m at night. Four specimens (22–45 mm ML) were captured in open nets that fished between 800 m and 900 m during the day and 700 and 800 m during the night.

In summary, the evidence suggests that some species of *Chiroteuthis* exhibit at least limited diel vertical migration. This is rather unexpected since they have small, weakly muscled mantles. It appears that the larvae of *C. calyx* at least, descend into deeper water as they increase in size until, by the time of metamorphosis, they have reached the depth of the subadult distribution.

Species of *Valbyteuthis* appear to be among the deepest living of all pelagic squid and apparently exhibit no diel vertical migration.

MASTIGOTEUTHIDAE

FIGURES 17, 29: BARS 8–11

The family Mastigoteuthidae consists of two genera. *Echinoteuthis* is recorded from only a few specimens and little is known of its distribution. *Mastigoteuthis* is a speciose genus, but meaningful data on vertical distributions are available for only a few species.

Mastigoteuthis pyrodes from California is represented by 27 specimens (Figure 17). Of the eight specimens captured during the daytime, none were taken above 600 m; two were captured in 600–700 m, five in 800–900 m, and one in 1000–1100 m. Thirteen specimens are recorded as twilight captures. Many of these captures undoubtedly occurred during daytime in trawls that extended into the twilight period. If these data are considered in conjunction with daytime captures, it appears that the upper limit of the daytime distribution is around 600 m. The lower limit is uncertain.

Of the five specimens captured at night; two were taken at 300–400 m, one at 400–500 m, and two at 600–700 m. Some upward movement during the night may occur, but the data are too meager to allow a definitive statement.

Fifteen specimens of *M. hjorti* have been captured off Bermuda. Closing net captures were made at night at 450 m (27 mm and 28 mm ML) and 510 m (30 mm ML). Open net nighttime captures were as follows; four specimens (29–37 mm ML) at 450–0 m, three (32–155 mm ML) at 750–0 m, and two (84 mm and 181 mm ML) at 760–0 m. Open net daytime captures of three specimens (27–115 mm ML) were made at 800–0 m, 950–0 m, and 1025–0 m.

Off Hawaii *Mastigoteuthis* sp. has been taken in closing nets at 700–875 m during the day (two specimens) and at night two specimens were cap-

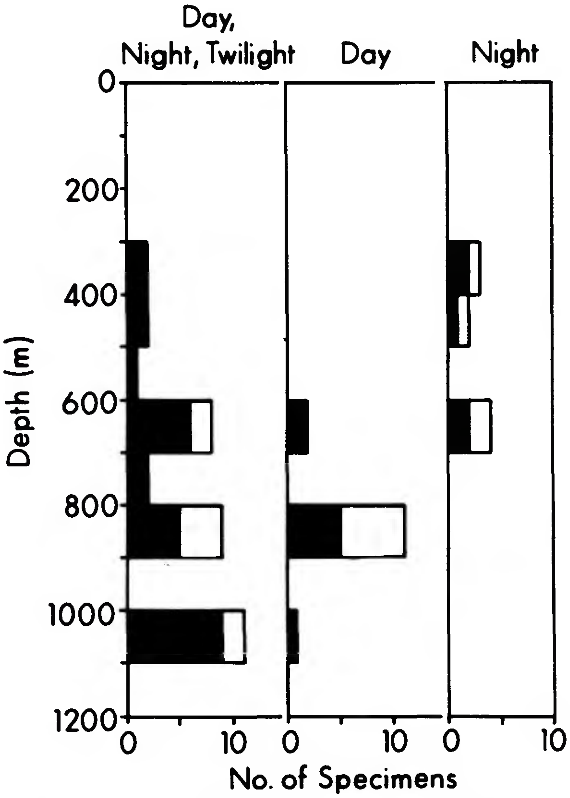

FIGURE 17.—Vertical distribution of *Mastigoteuthis pyrodes* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

tured from 260–325 m and two others from 690–770 m in closing nets. Five specimens (24–55 mm ML) have been taken in open nets that fished from 670–850 m during the day. Two specimens of *M. famelica* were taken during the day, probably at 810 m in a closing net that fished from 700–925 m. Eleven additional specimens (25–41 mm ML) were taken during the day in open nets between 700 and 800 m and single specimens were taken at 600–0 and 1100–0 m. A single specimen (37 mm ML) was captured in an open net at night at 375–0 m.

It appears from the species examined that members of this genus are deep-living animals with the upper limits of daytime distribution probably at 600–700 m depending on the locality. At night the captures suggest that while some individuals remain at the daytime depths, others spread upward into the 200–700 m zone.

PROMACHOTEUTHIDAE

FIGURE 29: BAR 12

The Promachoteuthidae has two known species in the single genus *Promachoteuthis*. The species *P. megaptera* is known from a single mutilated specimen taken by the CHALLENGER in an open bottom trawl that fished at 2440 m in the north Pacific. Two specimens of *Promachoteuthis* from Antarctic and southern Pacific waters were taken in open midwater trawls at 1391–0 m (10.5 mm ML) and 1830–0 m (17 mm ML), respectively. Two specimens (greater than 25 mm ML) were taken in open Engel trawls in the south Atlantic at 1550–0 m and 1900–0 m at night. Based on the anatomical features of this species, Roper and Young (1968:213) suggested that it is a deep-sea species; indeed, it is probably one of the deepest living of all squids.

BATOTEUTHIDAE

FIGURE 29: BAR 13

The Batoteuthidae is monotypic, known from only a few specimens (Young and Roper, 1968). Data on depths of capture in open nets are insufficient to verify vertical range; one larva (30 mm ML) was taken at 366 m during the day and juveniles and adults (51, 90, and 95 mm ML) were taken at 1257 m, 1866 m, and 2525 m during the night.

GRIMALDITEUTHIDAE

FIGURE 27: BAR 16

The Grimalditeuthidae is represented only by *Grimalditeuthis bomplandii*. The few previous records provide inadequate information on the vertical distribution of the species because depths of capture range from the surface to 2600 m. In the Atlantic four specimens (greater than 46 mm ML) have been taken at night in open nets at 1275–0 m, 1300–0 m, 1690–0 m, and 2100–0 m. Off Hawaii this species has been taken at 750–0 m (58 mm ML) and 1435–0 m (97 mm ML) at night, and at 1150–0 m (80 mm ML) during the day. We suspect that *G. bomplandii* is a deep-living species.

CRANCHIIDAE

FIGURES 18–20, 30: BARS 1–9

The Cranchiidae is a highly diversified group that contains numerous genera and species. The family is so diverse and so poorly known that we shall make no attempt to survey the distributional records of all the genera. We shall discuss only the species for which we have accumulated direct information.

Galiteuthis phyllura off California is represented by 182 specimens (Figure 18). This species undergoes a metamorphosis at about 60 mm ML. The larvae exhibit ontogenetic descent whereby increasingly larger larvae occupy successively greater depths. In the upper 100 m larvae from 1–10 mm ML (mean 7.5 mm ML) predominate; between 100–300 m the 10–30 mm ML size range (mean 23.4 mm ML) predominates; at 300–500 m the 20–40 mm ML size (mean 28.1 mm ML) predominates; and at 500–600 m the 30–50 mm ML size (mean 33.3 mm ML) predominates. The mean values for most of these size groups would be larger if contamination of each depth zone from overlying zones were eliminated.

At approximately 60 mm ML larval development is complete and the animals descend to 900 m or more as subadults (Figure 19). Twenty-one percent of the larval specimens less than 50 mm ML, however, were taken in the 1000–1200 m zone and may descend prematurely, although contamination may be partly responsible for this peculiar pattern. No indication of vertical migration exists for specimens smaller than 55 mm ML.

During the daytime only a single specimen larger than 55 mm ML was taken in water shallower than 900 m, one specimen was taken in 900–1000 m, three in 1000–1100 m, and seven in 1100–1200 m. When twilight captures are considered as well, it seems clear that the bulk of the subadult population is located below 900 m.

Only a small number of specimens was taken at night; three specimens were captured in the upper 200 m, seven in 500–600 m, and three in 1100–1200 m. The captures above 900 m indicate that some of the subadult population wander into the upper layers at night. Five of the seven specimens taken at 500–600 m at night are less than 100 mm ML; since this depth corresponds approximately to the maximum depth of larval occurrence, this may indicate that a tendency exists for some specimens to remain there after metamorphosis.

Off Hawaii, nine specimens (20–52 mm ML) of *G. pacifica* were taken in open nets that fished below 650 m (seven day captures and two night captures). Four additional specimens (25–258 mm ML) were taken during the day in closing nets between 650–800 m, and another specimen (42 mm ML) was captured in a closing net probably at 550 m (500–560 m range) during the day. In spite of the single record at 550 m, *G. pacifica* appears generally to occupy depths below 600 m during both day and night. This species undergoes meta-

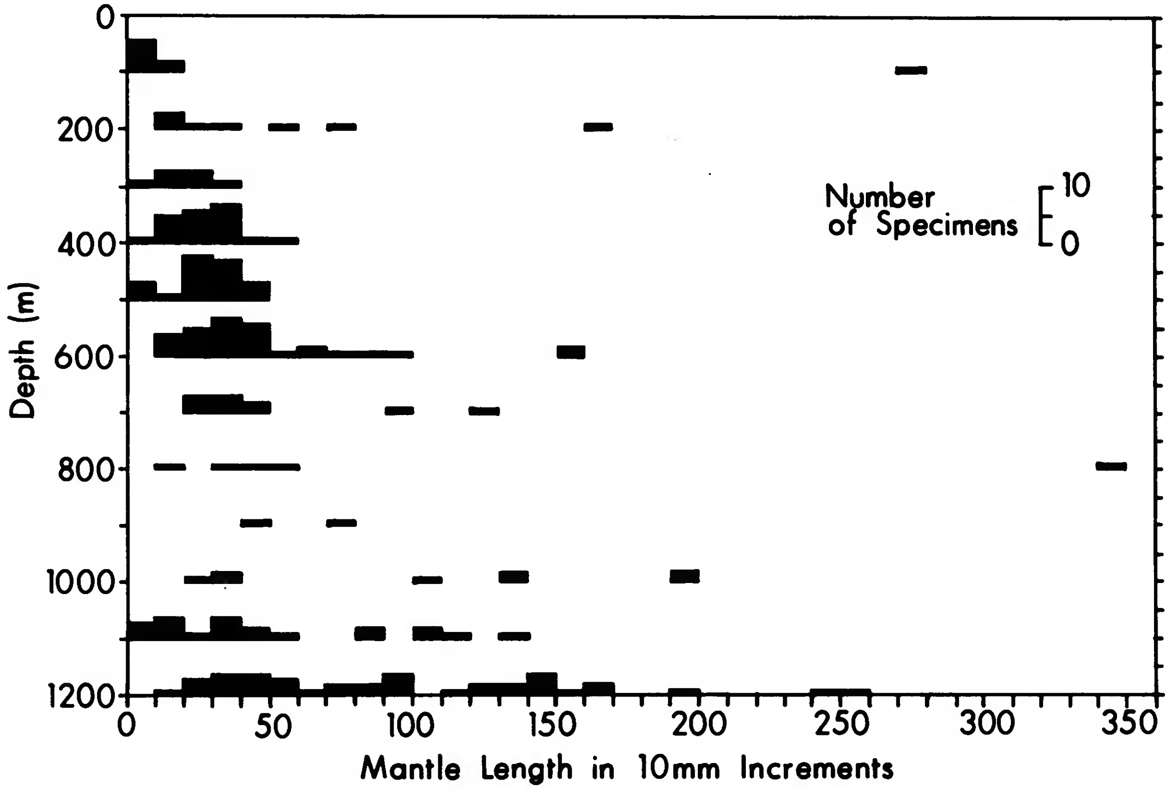

FIGURE 18.—Vertical distribution with respect to size-groups of *Galiteuthis phyllura* off southern California. (Black bar = number of specimens captured.)

morphosis at about 40–45 mm ML. Data are insufficient to show the existence of ontogentic descent.

Galiteuthis glacialis is restricted primarily to Circumpolar Deep Water in Antarctic waters (McSweeny, 1971:104). Based on open net data, McSweeny (1971) concluded that the vertical range of the species extends from 200 m to about 1400–1500 m; the bulk of the population lives between 600 and 1000 m. An indication of ontogenetic descent exists, since the mean capture depths for successively larger 10 mm size groups increase for animals of 20–90 mm ML. McSweeny also suggested that a diel vertical migration occurs; maximum daytime captures occur at 800–1000 m while maximum nighttime captures occur at 400–600 m. McSweeny's data indicate that, rather than a well-defined migration, the animals disperse at night into a broader range of depths since nighttime captures are relatively high between 200 and 1000 m.

In the California study 102 specimens of *Helicocranchia pfefferi* (10–70 mm ML) were used to plot vertical distribution (Figure 20). The specimens captured both during the day and night with open nets are well intermixed at all depth levels. No specimens were taken in the upper 100 m, 4 percent were captured between 100–200 m, 21 percent in 200–300 m, 38 percent in 300–400 m, 11 percent in 400–500 m, 12 percent in 500–600 m, 3 percent in 600–700 m, 8 percent in 700–800 m, and 4 percent below 800 m. The bulk of the captures (59 percent) occurs in the zone between 200 and 400 m. Eighty-seven percent of the specimens captured in this zone are 10–40 mm ML. Although only a small number of specimens (20)

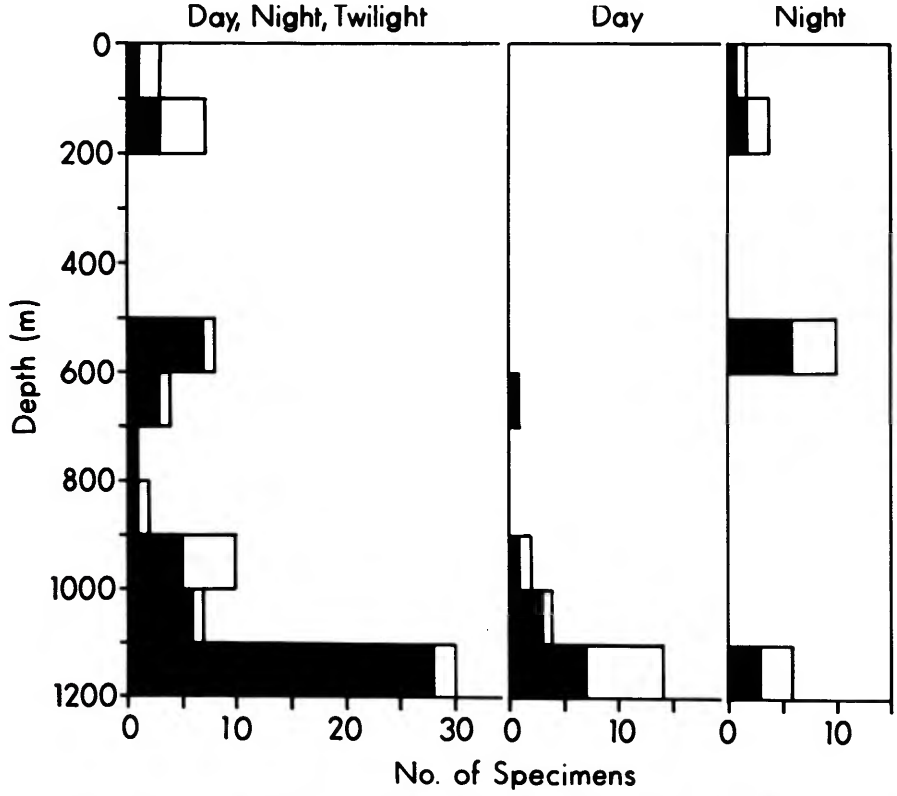

FIGURE 19.—Vertical distribution of subadult *Galiteuthis phyllura* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

was captured in the 400–600 m zone, 65 percent of these were over 40 mm ML. The data suggest that larger animals (i.e., over 40 mm ML) live in deeper water. A break in distribution lies at 600 m which may be the bottom of the vertical range of *H. pfefferi*. The deeper captures presumably are contaminants. No diel vertical migration occurs.

Records for seven larval specimens of *Taonius pavo* are available from Bermuda and Hawaii. Off Bermuda three specimens (35–43 mm ML) were captured in closing nets between 610–690 m during the day. Off Hawaii, four daytime captures (60–115 mm ML) were made in closing nets between 600 and 800 m.

Two specimens of *Bathothauma lyromma* (23 and 33 mm ML) were captured off Bermuda at 520 m at night in closing nets. Off Hawaii one specimen (80 mm ML) was taken in a closing net at night at 700–730 m and a mature female (100 mm ML) was captured in a closing net at 1015–1300 m during the day.

Leachia sp. off Bermuda is represented in our collections by 309 specimens that range from 4–50 mm ML. During the day 159 specimens (4–28 mm ML) were taken at 50 m and 12 specimens (25–50 mm ML) were taken at 60 m. At night 93 specimens (7–29 mm ML) were taken at 50 m; 36 specimens (5–24 mm ML) were captured at 100 m, and nine specimens (26–48 mm ML) were taken at 135–230 m. It is worth noting that most of the large specimens taken during the daytime were the deepest captures. No evidence of diel vertical movement exists.

Off Baja California, a specimen of *Leachia dislocata* (100 mm ML) was dipnetted at the surface at night.

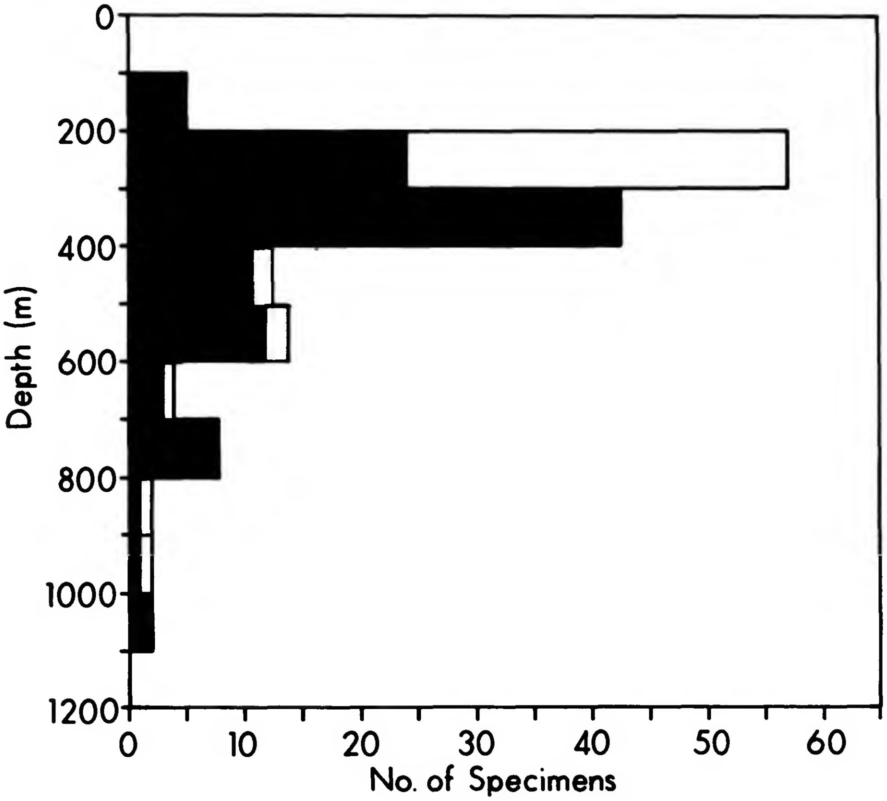

FIGURE 20.—Vertical distribution of *Helicocranchia pfefferi* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

Five specimens of *Phasmatopsis oceanica* (17–29 mm ML) were taken in closing nets off Bermuda during the day between 90 m and 200 m and three specimens (19–27 mm ML) were captured at night from 50–175 m. Off Hawaii, 97 specimens (8–55 mm ML; one at 130 mm ML) of *P. fisheri* were taken at night from 200–0 m, and five specimens, presumably contaminants, from 800–0 m. Daytime captures for this species are inconclusive.

Off Hawaii, 16 specimens of *Liocranchia valdiviae* have been captured in closing nets. Apparently 10–20 mm ML is the size range at which the larvae begin to assume the adult habitat. Eleven specimens less than 20 mm ML have been taken at scattered depths between 175 m and 750 m. Five specimens from 21–42 mm ML have been taken in closing nets from 650 m to about 1050 m. Sixty-eight specimens were taken in open nets of which 33 specimens larger than 21 mm ML were captured between 700 m and 1200 m. Twenty of these came from 700–800 m, five from 800–900 m, six from 900–1000 m, and two from 1000–1200 m. Day and night captures are intermixed for all specimens larger than 21 mm ML.

The species we have examined in the Cranchiidae exhibit several different patterns of vertical distribution. The juveniles, at least, of some species (e.g., *Leachia, Phasmatopsis*) live in near-surface waters. Some (e.g., *Helicocranchia*) occupy intermediate depths. Most species, however, live in deep water below 600–700 m (e.g., *Liocranchia, Galiteuthis, Taonius, Bathothauma*). At present no species has been shown to exhibit strong vertical migration. One distributional pattern appears to be prominant in the family: Many species exhibit ontogenetic descent, that is, in larval and juvenile stages, larger specimens inhabit progressively deeper waters. Where known, adults and subadults occupy the deepest waters.

Order VAMPYROMORPHA

VAMPYROTEUTHIDAE

FIGURES 21, 31: BAR 1

The vertical distribution of *Vampyroteuthis infernalis*, the only species in the order Vampyromorpha, has been extensively investigated by Pickford (1946, 1949). She (1946:25) states that the majority of specimens are found in water that has a salinity between 34.7 ‰ and 34.9 ‰ (maximum range 34.5–35.5 ‰), an oxygen content between 1.00 ml/L and 3.99 ml/L, a density (sigma-t) between 27.4 and 27.8 (maximum range 27.0–27.9), a temperature between 2.0° and 6.0° C (maximum range 1.73°–15.46° C). The species is most abundant between 1500 m and 2500 m in the Pacific Ocean and 1000–2000 m in the Atlantic Ocean.

Vampyroteuthis infernalis was the third most abundant species in the California study. Three hundred and eighty-five specimens were captured ranging in size from 8 mm to 110 mm ML (Figure 21). The daytime and nighttime captures intermingle at all depths, indicating that no vertical migration occurs. No specimens were taken in the upper 100 m, and only 2 percent were taken between 100 m and 400 m. This species is susceptible to entanglement in trawl nets, and very likely many of the records above 400 m represent contamination of this type from preceeding deeper trawls. Six percent of the specimens were captured between 400 m and 600 m, part of which may represent contamination and part stragglers from the main population. Forty-five percent of the captures occurred between 600 m and 800 m with those between 700 m and 800 m accounting for 34 percent of the captures. The 800–900 m zone accounts for 8 percent of the specimens, the 900–1000 m zone 15 percent, the 1000–1100 m zone for 16 percent, and the 1100–1200 m zone 6 percent. When catch per trawling effort is considered, peaks occur in the distribution at 700–800 m and at 900–1000 m. Sixty-five percent of the specimens with a mantle length less than 20 mm were captured deeper than 900 m, while 76 percent of the specimens with a mantle length of 20 mm or larger occur shallower than 900 m. This size is the point at which the larval fins begin to be resorbed. The larval forms, therefore, generally occupy a slightly deeper layer than the adults.

The upper limit of most of the captures is 600 m, and the lower limit probably is 1100 m or 1200 m. Even though the water off California between 1200 m and 2200 m (around the 2° C isotherm) would appear to be well suited to *V. infernalis*, according to previous studies, the species probably

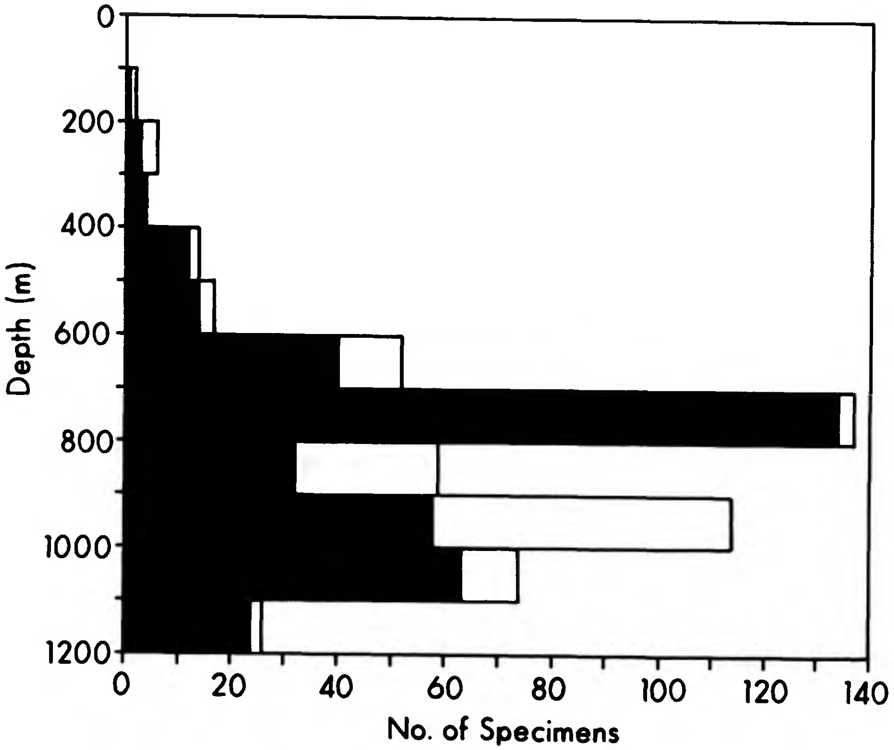

FIGURE 21.—Vertical distribution of *Vampyroteuthis infernalis* off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

is absent or at least not abundant in this zone. The vertical distribution falls within a temperature range of approximately 3°–6° C, a salinity variation of 34.4 ‰ to slightly over 34.5 ‰, a density (sigma-t) range of 27.1–27.5, and oxygen values of 0.3–0.8 ml/L. These values extend the limits for the majority of previously recorded specimens, for all parameters except temperature. These limits, however, are so broad that other features may be equally or more important in controlling the distribution of this species.

Off Bermuda, 12 specimens of *V. infernalis* were captured between 950 m and 1500 m in open nets. In the south Atlantic 175 specimens (18–94 mm ML) of *V. infernalis* were taken in open Engel trawls at night; 115 specimens were taken at 1300–2000 m, with the large majority at 1800–2000 m (13 tows), and 10 were taken in five tows that fished between 500 m and 1000 m. One tow captured 50 specimens at 640–0 m.

Order OCTOPODA

Suborder CIRRATA

CIRROTEUTHIDAE and STAUROTEUTHIDAE

FIGURES 22, 31: BARS 10, 11

Species in these families are rare in collections, and the systematics are very confused; relatively little is known of their distributions. Recently Roper and Brundage (1972) reviewed the depth records in the literature and added information based on deep-sea photographs. They concluded that *Cirroteuthis* spp., and probably some of the other cirrates as well, are benthopelagic, living just above, but not on, the ocean bottom (Figure 22). Records for species of *Cirroteuthis*, *Grimpoteuthis*, and *Stauroteuthis* indicate that the group as a whole extends from about 350 m to 5300 m. While a few species appear to live primarily shal-

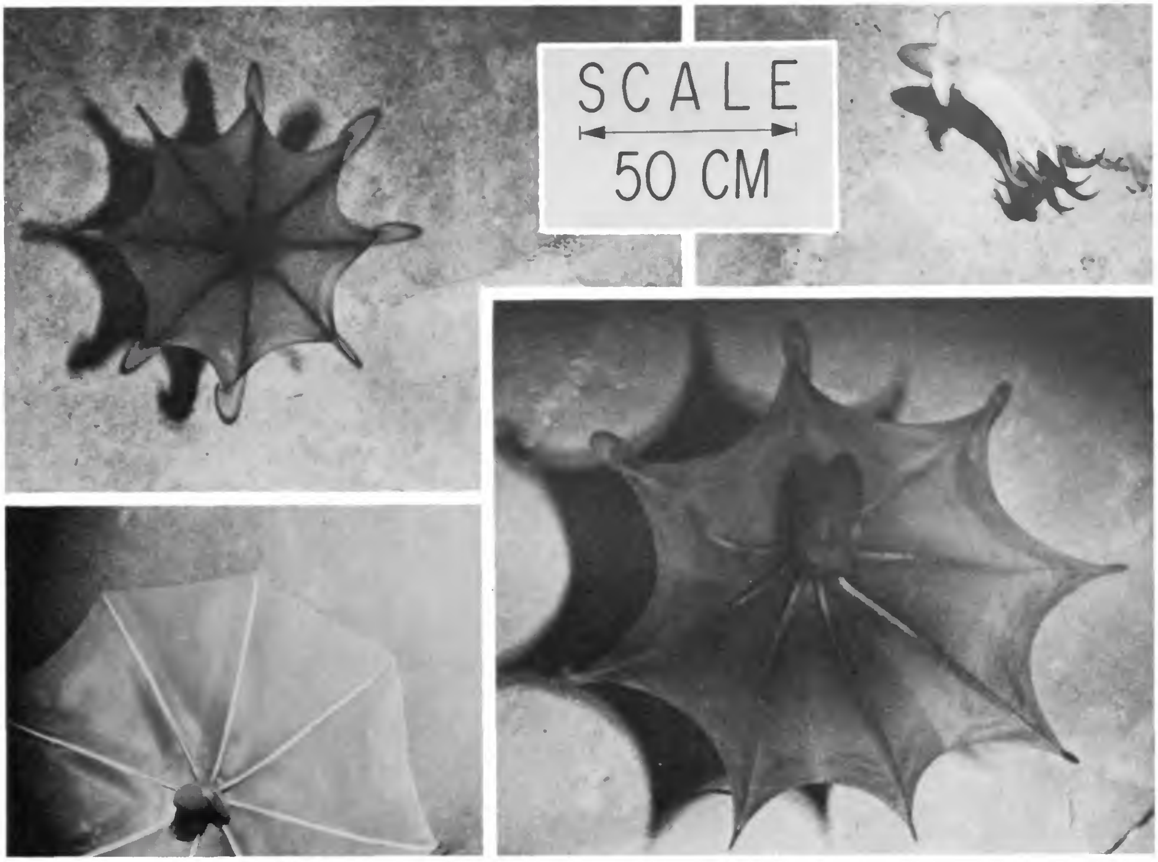

Figure 22.—Cirrate octopods near ocean bottom in Virgin Islands Basin, 3600–3950 m. Scale approximate. (After Roper and Brundage, 1972.)

lower than 1000 m, the large majority occur at depths in excess of 1000 m and many of these in excess of 2000 m (Robson, 1932:82–89). The photographic records of Roper and Brundage (1972) are concentrated in 3500–5200 m.

Cirrothauma murrayi, known from only a few specimens, is pelagic (Roper and Brundage, 1972: 14) and has been taken in open midwater nets at the following depths: 1500 m, 2900 m (night), 3600 m (day), and 4050 m (night). Specimens of this species are very fragile and are blind. The clear indication of deep-living habitat provided by anatomical and trawl data is partially offset by the capture of a specimen at the surface through the ice in the Arctic Ocean; this may, however, be an example of polar emergence of the widely distributed species.

OPISTHOTEUTHIDAE

The several species in this monotypic family, represented by *Opisthoteuthis*, all appear to be benthic forms; they are weak swimmers and seldom leave the bottom (Pereyra, 1965:436). Depth records range from 125–2251 m, but the great majority of captures come from 400–1000 m (see discussion in Roper and Brundage, 1972:16).

Pereyra (1965:430) reports that *Opisthoteuthis californiana* is distributed from 125–825 m, the shallower captures occurring in the northern end of its range. In addition, males of *O. californiana* appear to occupy shallower depths than females and to move into shallower water during the summer.

Suborder INCIRRATA

BOLITAENIDAE

FIGURES 23, 31: BARS 2, 3

Thore (1949) monographed the family Bolitaenidae and treated the horizontal and vertical distribution based on open net captures of one of the most common species, *Japetella diaphana*. He considered this species to be world-wide but latitudinally bounded by the 10° C isotherm at 200 m. Thore's data on the vertical distribution of *J. diaphana* indicated that young specimens less than 25 mm ML live between 100 m and 330 m, while larger specimens migrate to greater depths, with a lower limit between 3000 m and 4000 m.

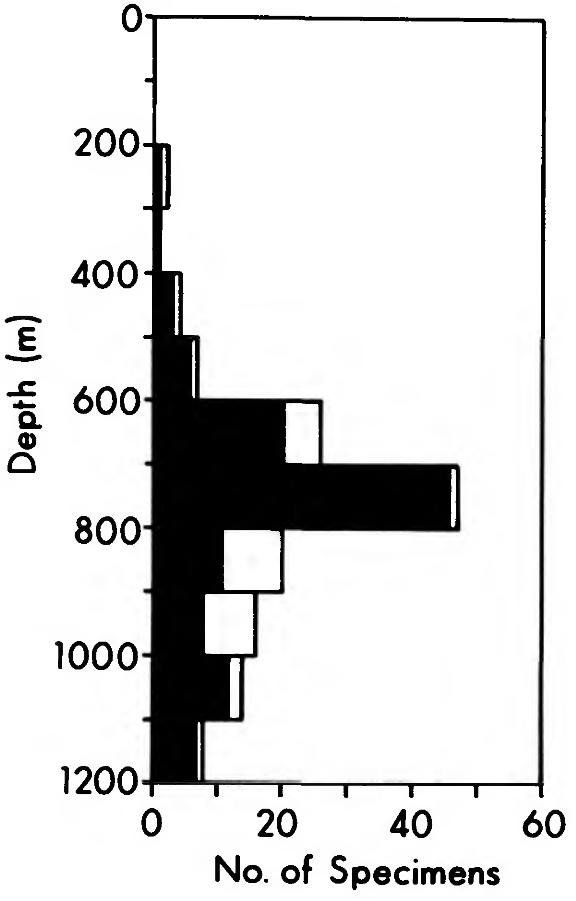

FIGURE 23.—Vertical distribution of *Japetella* sp. and *J. heathi*, off southern California. (Black bar = number of specimens captured; white bar = correction factor.)

Two species of *Japetella* occur off southern California. Nearly all specimens are *J. heathi*; however, since it is impossible to separate the two species at small sizes, their distributions are considered together. The 115 specimens (8–100 mm ML) captured in open nets were intermixed at all depths during the day and night (Figure 23).

No specimens were captured in the upper 200 m, 10 percent between 200 m and 600 m, 57 percent from 600–800 m, and 33 percent from 800–1200 m. All specimens captured shallower than 600 m were less than 20 mm ML and were nighttime captures. Below 600 m, 74 percent of the specimens less than 30 mm ML occur in the 600–800 m zone. This size category comprises over 80 percent of the total captures in the 600–800 m range. Specimens larger than 30 mm ML are evenly distributed from 600–1200 m. Therefore, nearly all the younger specimens seem to occupy a rather restricted vertical zone between 600–800 m, while the larger animals occur from 600 m to the depth limits of the sampling program and presumably occur in greater depths.

The genus *Bolitaena* consists of a single poorly known species, *B. microcotyla*. Off Hawaii a brooding female (35 mm ML) was taken in a closing net between 830 m and 975 m during the day (Young, 1972b).

Thore (1949:62) suggests that *Eledonella pygmaea* has a distribution similar to that of *Japetella diaphana*.

VITRELEDONELLIDAE

FIGURE 31: BAR 4

According to Thore's (1949) data, specimens of *Vitreledonella richardi* less than 100 mm ML occur in the upper 300 m, while those larger than 100 mm ML occur below 1000 m with a peak concentration at 1000–1050 m. Off Hawaii one specimen (23 mm ML) of *V. richardi* was captured in a closing net during the day between 615 m and

690 m. Off Bermuda four larval specimens less than 11 mm ML were captured in closing nets during the night and twilight at depths of 200–300 m.

AMPHITRETIDAE

FIGURE 31: BAR 5

This monotypic family consists of only *Amphitretus pelagicus*. Based on five captures, Thore (1949:55) reported that small specimens (20 mm ML and smaller) occur in the upper 133 m. Data of adults are inconclusive. One specimen (35 mm ML) was taken at night off Hawaii in a closing net at 240–260 m.

In the South Atlantic five specimens of *A. pelagicus* were captured at night in Engel trawls: one (20 mm ML) at 300–0 m, two (30 mm and 32 mm ML) at 600–0 m and 750–0 m, and two (34 mm and 52 mm ML) at 2000–0 m.

ALLOPOSIDAE

FIGURE 31: BAR 6

The Alloposidae consists of a number of nominal species, all of which have been considered as synonyms of *Alloposus mollis* in the review by Thore (1949). The vertical distribution of *A. mollis* presents a perplexing problem, since specimens have been recorded from the surface to as deep as 3180 m.

Thore (1949:71) reported that specimens from 7–400 mm ML, taken in open midwater nets, occurred from 0–333 m; specimens less than 80 mm ML were limited to the upper 33 m. In general, captures of both large and small specimens are concentrated in the near-surface waters from open pelagic nets (0–200 m) and at around 450–1000 m from the bottom trawls (Thore, 1949:71; Robson, 1932:84; Verrill, 1882b:366). The National Marine Fisheries Service, Hawaii, has captured as many as 26 large specimens of *A. mollis* in a single otter trawl that fished at 682 m (L. Burgess, per. comm.).

Thore (1949:72), concluded that the species is a cosmopolitan form that spends part of its life on the bottom and part in open water but always in association with landmasses.

The pelagic and benthic captures of this gelatinous octopod seem peculiar and require further investigation before we can gain an understanding of its vertical distribution.

TREMOCTOPODIDAE

FIGURE 31: BAR 8

The family is represented by *Tremoctopus violaceus* and possibly by *T. lucifer* Akimushkin, 1963. *Tremoctopus violaceus* is a pelagic cosmopolitan species in all warm and temperate waters of the world. Females attain a large size (200 mm ML; Kramer, 1937), but males are much smaller (about 20–30 mm ML). Most specimens recorded in the literature are from the surface of near-surface waters, with a few scattered to about 300 m (Robson, 1932:85).

Off Bermuda, a juvenile *T. violaceus* (6 mm ML) was captured in a closing net at 100 m during the day, 10 juveniles (5–10 mm ML) were captured at the surface at night, and one juvenile was taken at 250 m at night.

OCYTHOIDAE

FIGURE 31: BAR 9

Ocythoe tuberculata, the sole species in the family, has been recorded from scattered oceanic localities (Robson, 1932:85; Berry, 1955:219), but nowhere does it seem to be abundant. Females attain a large size (up to about 300 mm ML), but males remain small (about 20 mm ML) and apparently live within pelagic salps in near-surface waters (Hardwick, 1970). The species is pelagic and seems to inhabit the near surface waters, but nothing more can be stated about its vertical distribution.

ARGONAUTIDAE

FIGURE 31: BAR 7

The several species of *Argonauta*, the sole genus in the family, are all open ocean dwellers that inhabit warm waters of the world (Robson, 1932:85). Many records in the literature indicate a surface and near-surface habitat. We have captured spawning adult females (shell diameters greater than 200 mm) at the surface at night in the Florida Current.

Four juvenile males (5–8 mm ML) of *A. argo* were captured in closing nets between 50 m and 200 m off Bermuda. In the Mediterranean Sea in closing nets, six juvenile males and females (5–13 mm ML) and one adult female (72 mm ML) of *A. argo* were captured at the surface at night and one juvenile female (6 mm ML) was captured at 155 m at night.

The species of *Argonauta* inhabit the surface and near-surface waters.

Discussion

A complete analysis of the vertical distribution of pelagic cephalopods should include information concerning physical and biological parameters that may regulate species distributions. Of particular importance are the roles of light, temperature, productivity, competition and predation in regulating species distributions. Also, the relationships of species distributions to vertical faunal zones should be considered. Unfortunately, knowledge concerning vertical distribution in cephalopods is rudimentary and we are restricted to a general discussion of approximate habitats and day-night differences in distribution.

The information presented here reveals a variety of patterns of vertical distribution in pelagic cephalopods. The types of patterns presented below are not all mutually exclusive; some species may exhibit a combination of patterns. All patterns are not necessarily sharply delimited.

NEAR SURFACE DWELLERS.—A number of species are found at or near the surface of the ocean throughout the diurnal cycle. Apparently only a

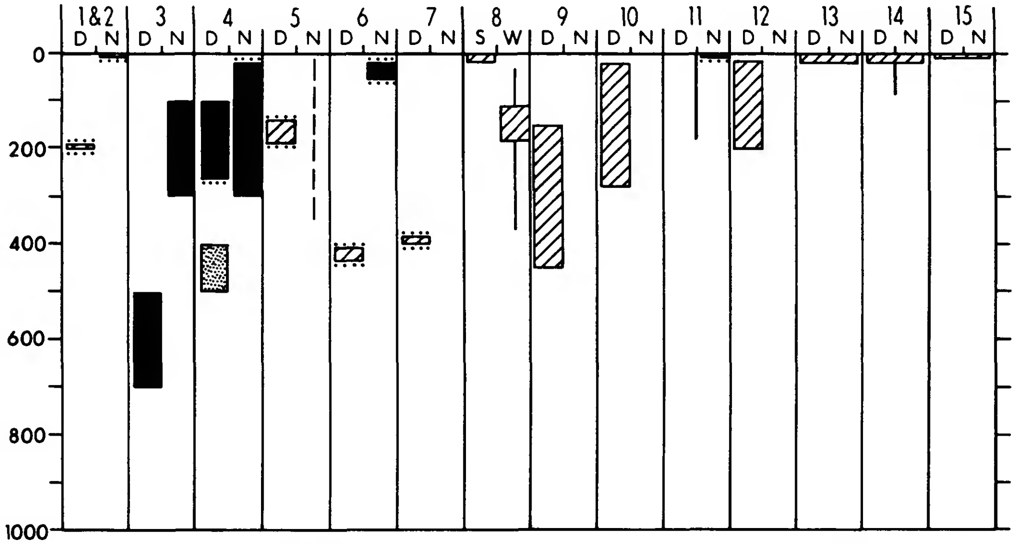

FIGURE 24.—Patterns of vertical migrations. 1 & 2 NAUTILIDAE: 1, 2, *Nautilus macromphalus* and *N. pompilius*, various localities. 3 SPIRIULIDAE: *Spirula spirula*, off Canary Islands. 4–7 HETEROTEUTHINAE: 4, *Heteroteuthis dispar*, off Canary Islands and Mediterranean; 5, *Stoloteuthis leucoptera*, off eastern United States (time of bottom trawl captures assumed to be day); 6, *Stoloteuthis maoria*, off New Zealand (time of bottom trawl captures assumed to be day); 7, *Nectoteuthis pourtalesi*, off Florida (time of bottom trawl captures assumed to be day). 8–14 LOLIGINIDAE: 8, *Loligo pealeii*, off eastern United States; 9, *Loligo forbesi*, Catalane Sea (time of capture assumed to be day); 10, *Loligo vulgaris*, off northwest Africa; 11, *Loligo plei*, tropical western Atlantic; 12, *Alloteuthis media*, Mediterranean (time of capture assumed to be day); 13, *Sepioteuthis sepioidea*, tropical western Atlantic; 14, *Lolliguncula brevis*, off tropical western Atlantic. 15 PICKFORDIATEUTHIDAE: *Pickfordiateuthis pulchella*, tropical western Atlantic. (D = day, N = night, S = summer, W = winter; see pp. 2–3 for explanation of symbols.)

single species, *Onykia caribaea*, presently qualifies as a member of the neuston, living at the ocean surface. Some other members of *Onykia* for which data are lacking may also occupy this habitat. Other cephalopods in this category occur primarily in the upper 50 m or so during the day and night. This group includes the octopods, *Argonauta* spp., *Tremoctopus violaceus*, and *Ocythoe tuberculata*, as well as some of the squid such as *Thysanoteuthis rhombus*.

Other shallow-living species avoid the near-surface waters during the day and move into these waters during the night. These shallow diel migrators include *Nautilus pompilius*, *N. macromphalus*, *Todarodes pacificus*, and probably many of the loliginid species.

Among the Ommastrephidae, a number of open ocean species (e.g., *O. caroli*) seem to occur primarily in the upper few hundred meters during the day and night. Some individuals, however, apparently roam into great depths. Species that exhibit roaming activities are powerful swimmers for which data are difficult to obtain, and the extent and magnitude of roaming are uncertain.

First Order Diel Vertical Migrators.—Many species live at moderate depths during the daytime and migrate into the upper 200 m at night. All members of the Enoploteuthidae, where known, are first order diel vertical migrators. During the day these species occur primarily between 300 m and 600 m, and at night they are found in the upper 200 m. Within these zones, the distribution of a given species may be considerably more restricted (e.g., *Pyroteuthis margaritifera*). At least one member of the Lycoteuthidae, *Selenoteuthis scintillans*, exhibits the same pattern of distribution, and data suggest that members of the Cycloteuthidae also exhibit this pattern.

Strong diel vertical migration from great depths is indicated by data for only a single genus. Species of *Brachioteuthis* inhabit deep water (about 900–1000 m) during the day and ascend into the upper 200 m at night.

Ctenopteryx sp. seems to occupy an inter-

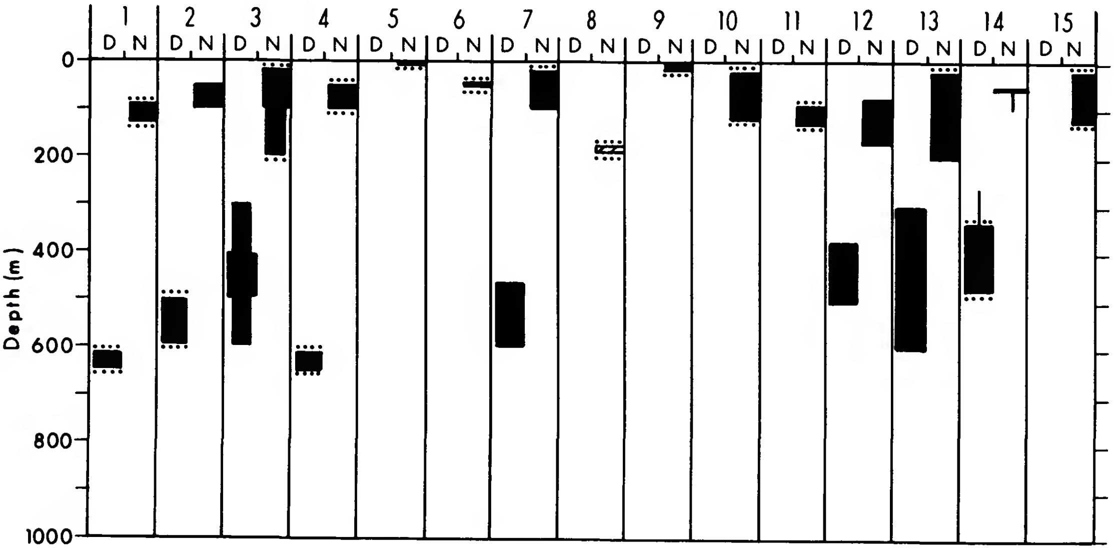

Figure 25.—Patterns of vertical migrations. 1 Lycoteuthidae: *Selenoteuthis scintillans*, off Bermuda. 2–15 Enoploteuthidae: 2, *Abràliopsis* sp., off Hawaii; 3, *Abraliopsis felis*, off California; 4, *Abraliopsis pfefferi*, off Bermuda; 5, *Abralia veranyi*, off Madeira; 6, *Abralia redfieldi*, off Bermuda; 7, *Abralia trigonura*, off Hawaii; 8, *Abralia astrostica*, off Hawaii; 9, *Watasenia scintillans*, off Japan; 10, *Enoploteuthis anapsis*, various localities; 11, *Enoploteuthis* sp., off Bermuda; 12, *Pyroteuthis margaritifera*, off Bermuda; 13, *Pterygioteuthis gemmata*, off Califorina; 14, *Pterygioteuthis giardi*, off Bermuda; 15, *Thelidioteuthis alessandrinii*, several localities. (D = day, N = night; see pp. 2–3 for explanation of symbols.)

mediate position between the few migrators from great depths and the many from mid-depths. It migrates from 600–800 m into the upper 150 m.

SECOND ORDER DIEL VERTICAL MIGRATORS.—At night, some species desert their daytime depths and migrate toward the surface but generally occupy deeper waters than first order migrators. For instance, *Spirula spirula* moves from 500–700 m in the day to 200–300 m at night, and *Histioteuthis heteropsis* moves from 400–800 m (peak at 500–700 m) during the day to the upper 400 m at night, with a peak at 300–400 m. Second order migrators also appear to occupy somewhat greater depths during the day than most first order migrators.

DIEL VERTICAL SHIFTERS.—Some species shift upward slightly at night with the nighttime distribution overlapping the daytime distribution. Several species of *Gonatus* shift from 400–800 m during the day to 300–500 m at night.

DIEL VERTICAL SPREADERS.—The nighttime vertical distribution in some species not only encompasses the daytime levels, but spreads well beyond the daytime limits. For example, *Octopoteuthis deletron* appears to occupy depths of 200–400 m during day and at night spreads out over depths from near the surface to about 500 m. Although the data are insufficient, we suspect that species of *Mastigoteuthis* are also spreaders.

NONMIGRATORS.—Many species exhibit no diel changes in vertical distribution. Nonmigrators include species from near-surface waters, as men-

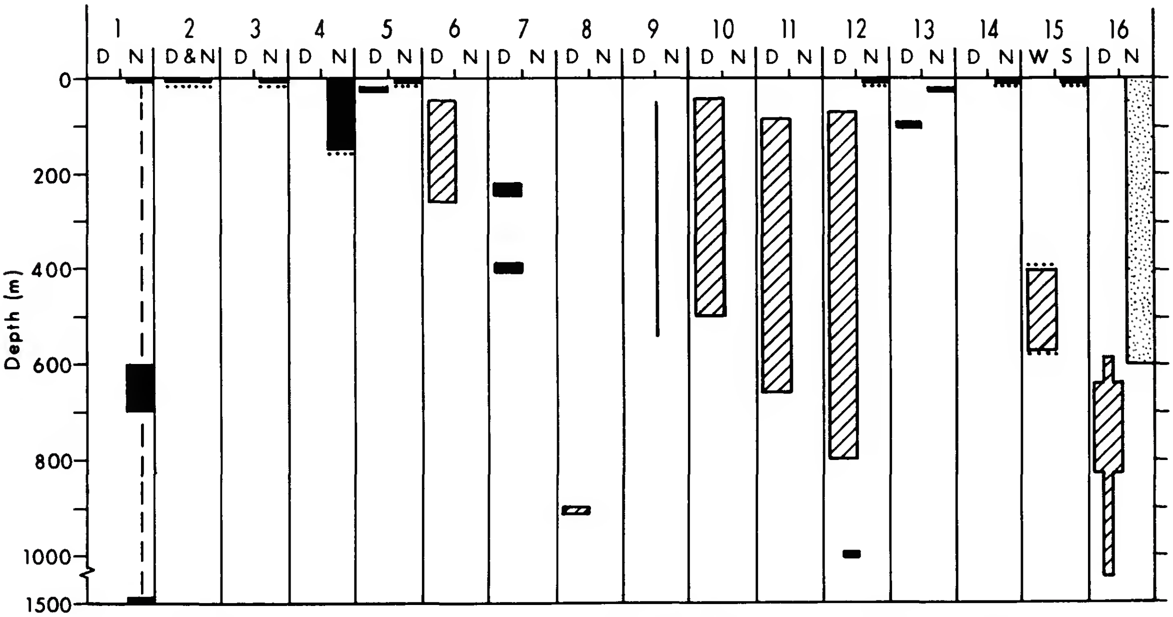

FIGURE 26.—Patterns of vertical migrations. 1–16 OMMASTREPHIDAE: 1, *Ommastrephes caroli*, central Atlantic; 2, *Ommastrephes bartramii*, several localities and *Dosidicus gigas*, off western South America; 3, *Symplectoteuthis oualaniensis* and *S. luminosa*, several localities; 4, *Hyaloteuthis pelagica*, off Bermuda; 5, *Illex illecebrosus*, off Newfoundland; 6, *Illex illecebrosus*, off the Chesapeake Bight, eastern United States; 7, *Illex illecebrosus?*, off Cape Hatteras; 8, *Illex* sp., off Miami, Florida; 9, *Illex oxygonius*, western Atlantic; 10, *Illex coindetii*, various localities in western Atlantic and Mediterranean (time of capture assumed to be day); 11, *Todaropsis eblanae*, various localities (time of capture assumed to be day); 12, *Todarodes sagittatus*, various localities; 13, *Todarodes pacificus*, off Japan; 14, *Nototodarus sloani gouldi*, off Australia; 15, *Nototodarus hawaiiensis*, off Hawaii; 16, *Ornithoteuthis antillarum*, various localities. (D = day, N = night, W = winter, S = summer, D&N = combined day and night captures (no marked diel differences in distribution); see pp. 2–3 for explanation of symbols.)

tioned above, as well as species from mid-depths and from great depths. For example, *Helicocranchia pfefferi* occupies the same mid-depths (200–600 m) during both the day and night. Nonmigrators are more prevalent in great depths than in mid-depths. For instance, species of *Bathyteuthis, Valbyteuthis, Japetella,* and *Vampyroteuthis infernalis* are deep-living nonmigrators.

VERTICAL WANDERERS.—Individuals of some deep-living species occasionally are found during the night considerably above the normal range. This pattern is displayed by *Galiteuthis phyllura* which normally occurs below 900 m, but during the night individuals may wander upward as far as the upper 100 m.

SPECIES ASSOCIATED WITH THE OCEAN BOTTOM.—

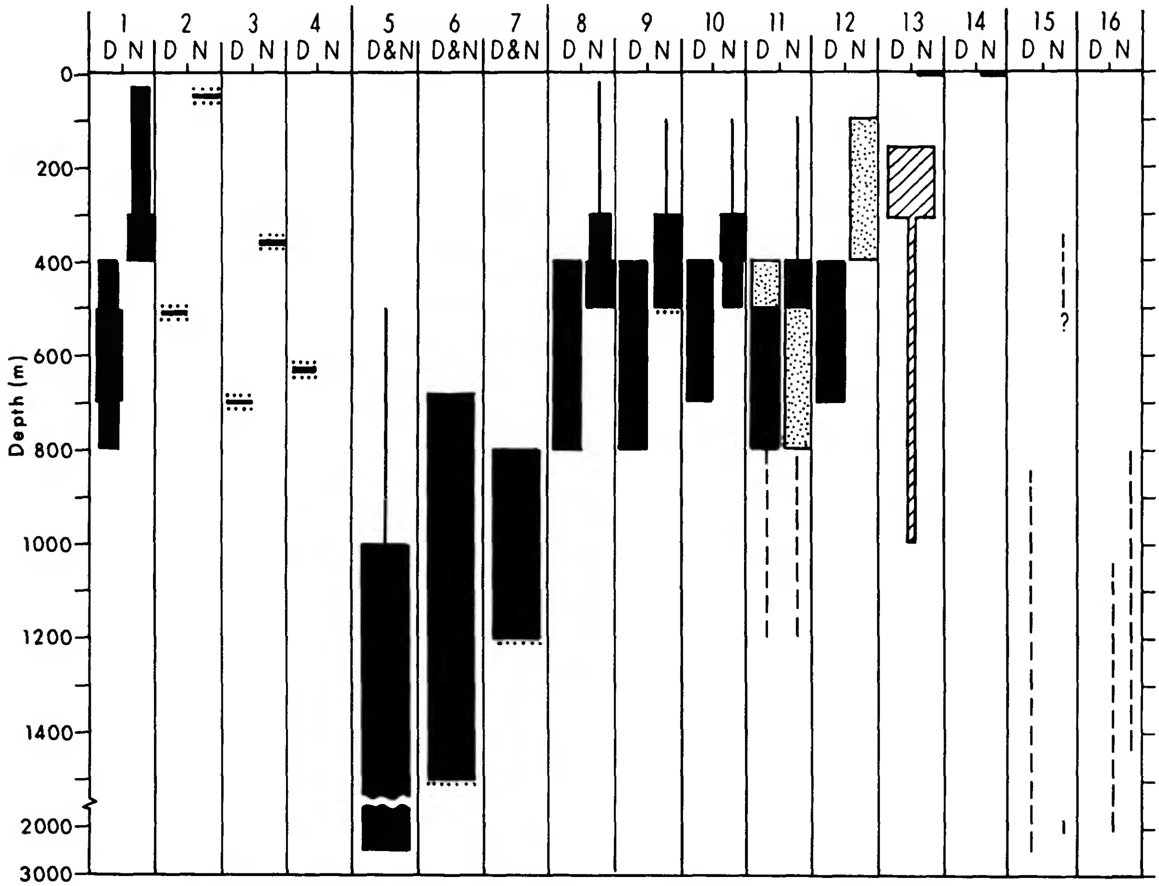

FIGURE 27.—Patterns of vertical migrations. 1–4 HISTIOTEUTHIDAE: 1, *Histioteuthis heteropsis,* off California; 2, *Histioteuthis dofleini,* off Bermuda; 3, *Histioteuthis meleagroteuthis,* off Bermuda; 4, *Histioteuthis corona,* off Bermuda. 5–7 BATHYTEUTHIDAE: 5, *Bathyteuthis abyssicola,* Antarctic waters; 6, *Bathyteuthis bacidifera,* tropical eastern Pacific; 7, *Bathyteuthis berryi,* off California. 8–14 GONATIDAE: 8, *Gonatus onyx,* off California; 9, *Gonatus californiensis,* off California; 10, *Gonatus pyros,* off California; 11, *Gonatus berryi,* off California; 12, *Gonatopsis borealis,* off California; 13, *Berryteuthis magister,* near Auke Bay, Alaska; 14, *Berryteuthis anonychus,* off Oregon. 15 JOUBINITEUTHIDAE: *Joubiniteuthis portieri,* various localities (shallow records are assumed to be nighttime captures). 16 GRIMALDITEUTHIDAE: *Grimalditeuthis bomplandii,* various localities. (D = day, N = night, D&N = combined day and night captures (no marked diel differences in distribution); see pp. 2–3 for explanation of symbols.)

A surprisingly large number of pelagic cephalopods live at least part of the time near the ocean bottom; these include shallow as well as moderately deep-living forms. Some species of the Heteroteuthinae (e.g., *Stoloteuthis maoria*) appear to belong to this category, as well as many species of loliginids (e.g., *Loligo pealeii* and *L. vulgaris*) and some ommastrephids, onychoteuthids, gonatids and mastigoteuthids.

SPECIES EXHIBITING ONTOGENETIC DESCENT.—Several species occupy progressively greater depths during successive stages in their life history. This is most apparent in species that have larvae which attain an unusually large size. For example, larval *Chiroteuthis calyx* with increasing size gradually descend from the upper 100 m to 500–700 m where they undergo metamorphosis at a mantle length of 50–60 mm. Many cranchiids exhibit a similar pattern (e.g., *Galiteuthis phyllura, Helicocranchia pfefferi*, and *Phasmatopsis fisheri*).

In contrast to this gradual ontogenetic descent, nearly all other species of pelagic cephalopods demonstrate a different type of ontogenetic descent; larvae occur in near surface waters and at a particular size abruptly descend to the adult habitat. An exception to this pattern occurs in *Vampyroteuthis infernalis* where the young occupy greater depths than the adults.

Some of the above patterns seem to correlate approximately with familial boundaries, although many exceptions exist. Most species that live in the upper 800 m exhibit some type of diel change in vertical distribution. Most species that live primarily below 800 m do not exhibit diel variations in vertical distribution. Apparently very few species live below 1000 m.

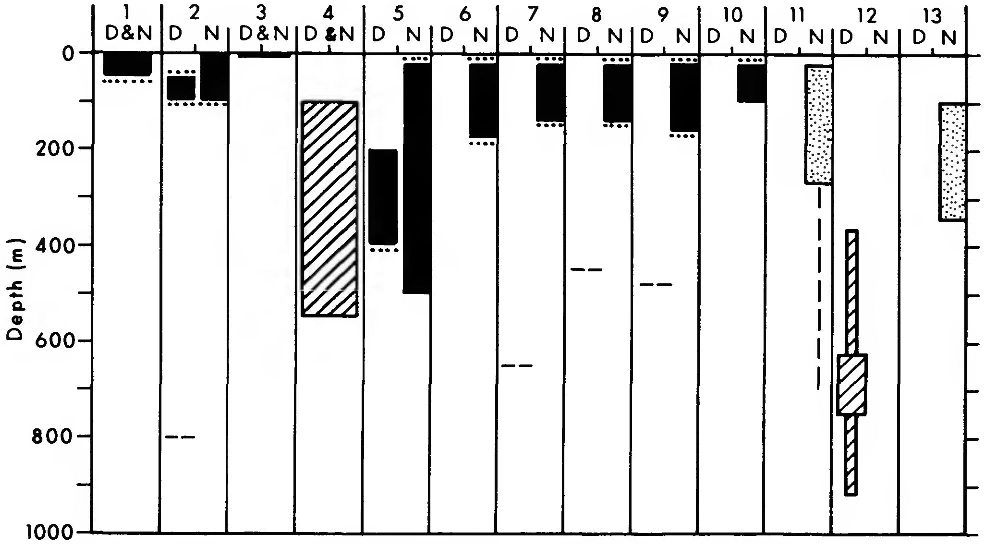

FIGURE 28.—Patterns of vertical migrations. 1. THYSANOTEUTHIDAE: *Thysanoteuthis rhombus*, various localities. 2–4 ONYCHOTEUTHIDAE: 2, *Onychoteuthis banksii*, off Bermuda and Mediterranean; 3, *Onykia caribaea*, various localities; 4, *Moroteuthis robusta*, off western North America. 5–6 OCTOPOTEUTHIDAE: 5, *Octopoteuthis deletron*, off California; 6, *Taningia danae*, various localities. 7–9 CYCLOTEUTHIDAE: 7, *Cycloteuthis sirventi*, various localities; 8, *Discoteuthis discus*, various localities; 9, *Discoteuthis laciniosa*, various localities. 10 CTENOPTERYGIDAE: *Ctenopteryx* spp., various localities. 11–13 LEPIDOTEUTHIDAE: 11, *Lepidoteuthis grimaldii*, various localities; 12, *Pholidoteuthis adami*, Gulf of Mexico, Caribbean Sea, and northeastern South American waters; 13, *Tetronychoteuthis dussumieri*, various localities. (D = day, N = night, D&N = combined day and night captures (no marked diel differences in distribution); see pp. 2–3 for explanation of symbols.)

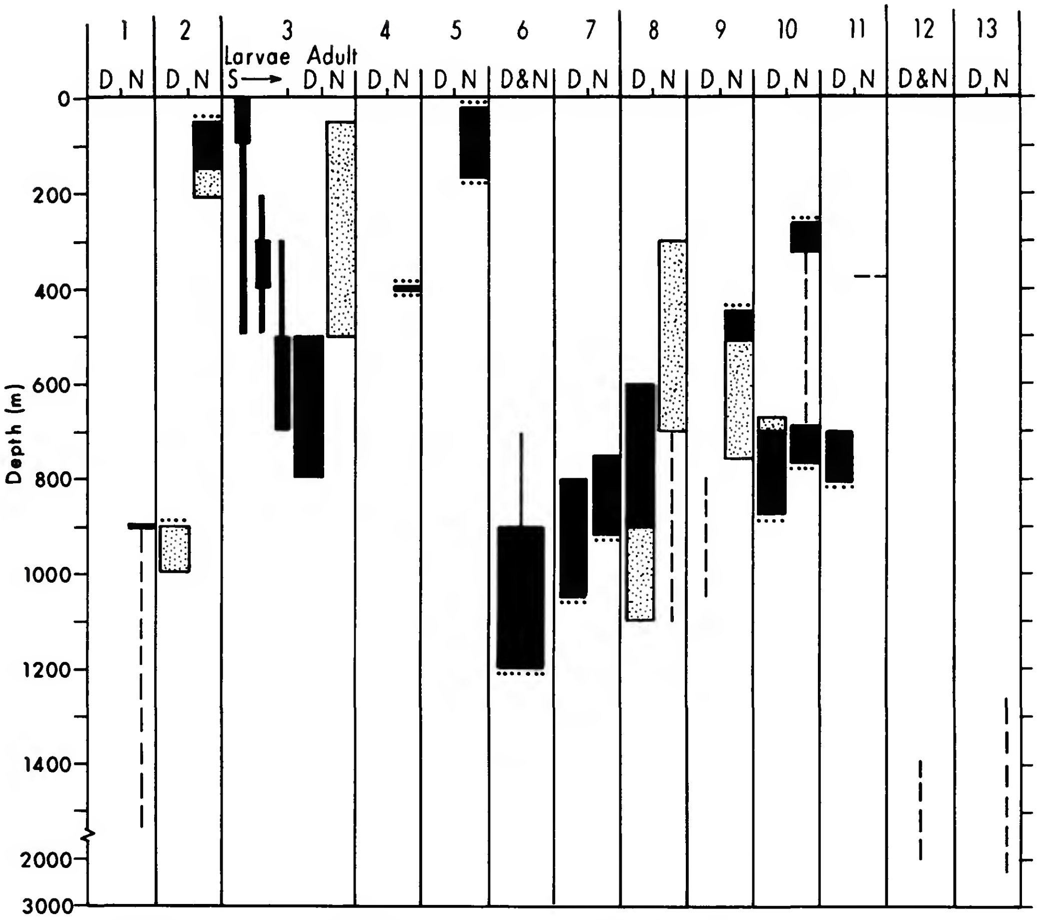

FIGURE 29.—Patterns of vertical migrations. 1 NEOTEUTHIDAE: *Neoteuthis* sp., eastern tropical Atlantic and Gulf of Mexico. 2 BRACHIOTEUTHIDAE: *Brachioteuthis* spp., off Hawaii and Mediterranean. 3–7 CHIROTEUTHIDAE: 3, *Chiroteuthis caylx*, off California; 4, *Chiroteuthis veranyi*, Mediterranean; 5, *Chiroteuthis* spp., off Hawaii and Bermuda; 6, *Valbyteuthis oligobessa*, off California; 7, *Valbyteuthis* sp., off Hawaii. 8–11 MASTIGOTEUTHIDAE: 8, *Mastigoteuthis pyrodes*, off Califronia; 9, *Mastigoteuthis hjorti*, off Bermuda; 10, *Mastigoteuthis* sp., off Hawaii; 11, *Mastigoteuthis famelica*, off Hawaii. 12 PROMACHOTEUTHIDAE: *Promachoteuthis* sp., various localities. 13 BATOTEUTHIDAE: *Batoteuthis scolops*, Antarctic waters. (D = day, N = night, D&N = combined day and night captures (no marked diel differences in distribution), S→ = size of individuals increase toward the right; see pp. 2–3 for explanation of symbols.)

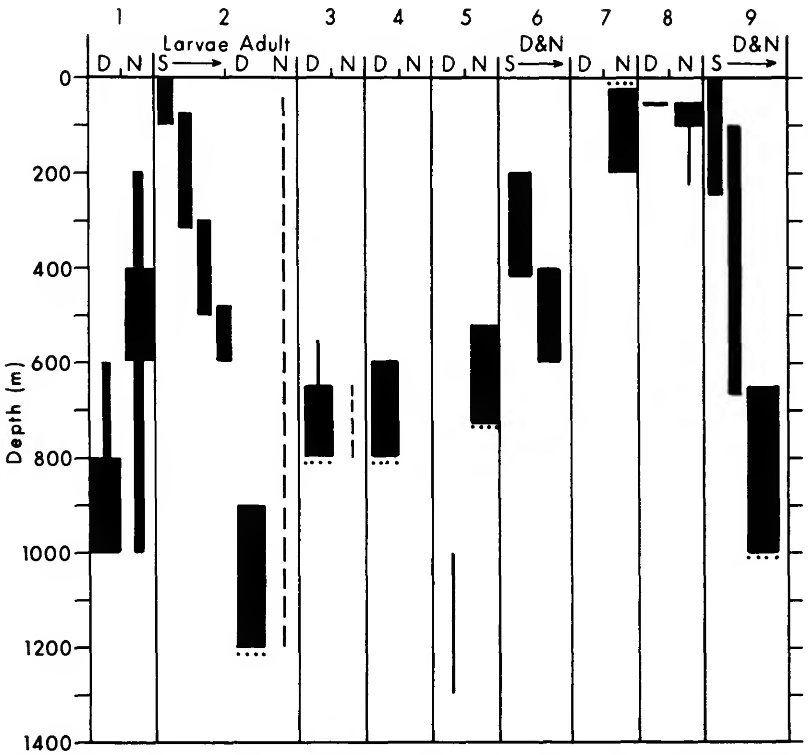

FIGURE 30.—Patterns of vertical migrations. 1–9 CRANCHIIDAE: 1, *Galiteuthis glacialis*, Antarctic waters; 2, *Galiteuthis phyllura*, off California; 3, *Galiteuthis pacifica*, off Hawaii; 4, *Taonis pavo*, off Bermuda and Hawaii; 5, *Bathothauma lyromma*, off Bermuda and Hawaii; 6, *Helicocranchia pfefferi*, off California; 7, *Phasmatopsis fisheri*, off Hawaii; 8, *Leachia* sp., off Bermuda; 9, *Liocranchia valdiviae*, off Hawaii. (D = day, N = night, S→ = size of individuals increases to the right, D&N = combined day and night captures (no marked diel differences in distribution); see pp. 2–3 for explanation of symbols.)

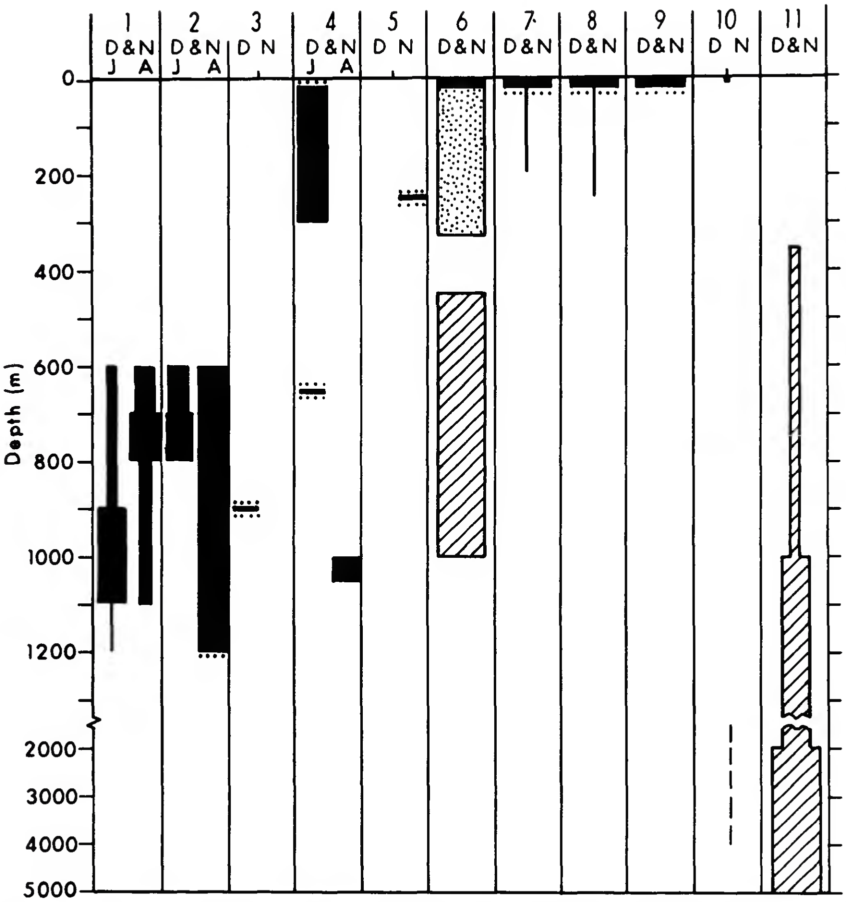

FIGURE 31.—Patterns of vertical migrations. 1 VAMPYROTEUTHIDAE: *Vampyroteuthis infernalis,* off California. 2–3 BOLITAENIDAE: 2, *Japetella* sp. and *J. heathi,* off California; 3, *Bolitaena microcotyla,* off Hawaii. 4 VITRELEDONELLIDAE: *Vitreledonella richardi,* various localities. 5 AMPHITRETIDAE: *Amphitretus pelagicus,* off Hawaii (consists of juveniles and larvae only). 6 ALLOPOSIDAE: *Alloposus mollis,* various localities. 7 ARGONAUTIDAE: *Argonauta* spp., various localities. 8 TREMOCTOPODIDAE: *Tremoctopus violaceus,* various localities. 9 OCYTHOIDAE: *Ocythoe tuberculata,* various localities. 10 CIRROTEUTHIDAE: *Cirrothauma murrayi,* various localities. 11 CIRRATA: most cirrate octopods other than *Cirrothauma* and opisthoteuthids, various localities. (D = day, N = night, D&N = combined day and night captures (no marked diel differences in distribution), J = juveniles, A = adults; see pp. 2–3 for explanation of symbols.)

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