VERTICAL DISTRIBUTION AND PHOTOSENSITIVE VESICLES OF PELAGIC CEPHALOPODS FROM HAWAIIAN WATERS

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ABSTRACT

Vertical distribution data were obtained for 47 species of pelagic cephalopods off Oahu, Hawaii. Peaks in species richness occurred at 500-800 m during the day and in the upper 300 m at night. Over 80% of the individuals occurred in the upper 250 m at night. Approximately 60% of the species underwent diel vertical migration, and most of these migrated into the upper 250 m. In five of nine groups of closely related species, clear differences in habitat were found.

Deepwater spawning appeared to occur in a variety of cephalopods. Two of the bathypelagic octopods brooded their young at or above the upper limit of the remaining adult population. In doing so, the extent of the upward migration of newly hatched individuals was reduced.

Photosensitive vesicles occurred in all species. These organs probably detect downwelling daylight for regulating vertical migration and counterillumination. The vesicles also appeared to form an elaborate system for monitoring bioluminescent light from the animal's own photophores, from within the mantle cavity, and from other animals located outside the visual field.

Cephalopods must occupy a wide variety of ecological roles in the pelagic realm of the open ocean: the highest diversification of families and genera is found in this environment. In order to understand these roles, the vertical distribution of these animals must be determined. A number of papers have treated various aspects of the vertical distribution of oceanic cephalopods (e.g., Pearcy 1965; Clarke 1969; Roper 1969; Gibbs and Roper 1971; Clarke and Lu 1974, 1975; Lu and Clarke 1975a, b; Roper and Young 1975). Their vertical habitats, however, remain poorly known.

Data on the vertical distribution of cephalopods is difficult to obtain: many species are uncommon, and some avoid small trawls. In this study an opening-closing net (modified Tucker trawl) provided unambiguous depth data, and a slightly larger open net (3-m Isaacs-Kidd midwater trawl) added considerable additional data; nevertheless, fast-swimming species were poorly sampled.

Extraocular photoreceptive organs, the photosensitive vesicles, were examined in each species for clues that would indicate the role of light in regulating vertical distribution patterns. The organs in squid, known as the parolfactory photosensitive vesicles, lie near the brain within the confines of the cephalic cartilage. In octopods the organs, known as epistellar photosensitive vesicles, lie within the mantle cavity adjacent to the stellate ganglia. The photosensitive vesicles are paired organs. Each organ, as the name implies, is generally composed of a large number of small vesicles. The individual vesicles contain photosensitive cells similar to those of the retina, and their photoreceptive nature has been well established (Nishioka et al. 1966; Mauro and Baumann 1968; Mauro 1977). The specific functions of the photosensitive vesicles are unknown in both neritic and oceanic cephalopods although many suggestions have been made (see Packard 1972).

Several papers discussing the relationship of vertical distribution to eye structure, bioluminescence and/or development of photosensitive vesicles in selected species have already appeared (Young 1972a, 1973, 1975a, c, d, 1977). Some data on distribution taken during the initial phases of this program have been published by Roper and Young (1975). This paper examines the vertical distribution of all pelagic cephalopods taken off Hawaii and the morphology and orientation of their photosensitive vesicles.

MATERIALS AND METHODS

Specimens were collected off the island of Oahu in the Hawaiian archipelago at long. 158°20′W, lat. 21°20′N over depths between 1,500 and 4,000 m. Collections were made from September 1969 to November 1974 primarily from the RV *Teritu*. Over 3,300 specimens were taken in horizontal tows during about 1,000 h of trawling time.

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Cephalopods were collected primarily with two types of nets: a 3-m opening-closing modified Tucker trawl and a 3-m Isaacs-Kidd midwater trawl (IKMT). Details of the trawling with the Tucker trawl are given by Walters (1976). When the Tucker trawl failed to close or close completely, the trawl was considered an open tow. Tows usually were made at 5 to 6 km/h for a period of 3 h. Twilight periods were generally avoided. Tows made with net closed indicated the catch contained almost no contamination. Contamination from previous tows was minimized by carefully cleaning the net after each tow. The trawl tended to wander vertically when open; this was most severe in deep tows. During the latter part of the program, acoustic depth telemeters allowed trawl depths to be continuously adjusted and greatly reduced wandering. The distribution figures indicate the extent of this wandering. Trawl depths usually were determined with a time-depth recorder attached to the trawl.

Clarke (1973) discussed trawling methods with the IKMT. The trawl was lowered quickly then towed horizontally at 5 to 6 km/h for usually 2 h. Retrieval was rapid with the ship moving slowly ahead. Vertical wandering of the net was not as serious as with the Tucker trawl. All specimens captured with the IKMT were assumed to come from the modal trawling depth of the net, or if no clear mode was present, from the midpoint of the effective vertical range of the tow. The occasional capture of a specimen during setting or retrieval of a net results in an anomalous depth record below the animal's normal habitat. Contamination of the catch by animals from previous tows occasionally occurred with the IKMT. This contamination is especially serious as the error may be impossible to detect.

IKMT data for a few of the most abundant species are presented both as catch per trawling effort and as actual catch figures (Table 1). The remaining distribution figures are designed to show animal size vs. depth relationships and to indicate the precision and reliability of the data (e.g., fishing range of the tow, open or opening-closing tow). As a result, corrections in the data for unequal sampling at various depths could not be made. This bias was especially critical at depths <400 m during the day and at depths >1,000 m during the day and night where sampling was low. The magnitude of this error can be determined from Table 2, which lists sampling time in each 100-m depth interval.

Depth data for most species taken over the entire trawling period have been combined. Therefore, short-term variation in depth distributions may be obscured. Where sufficient data exist to determine general distribution patterns based on Tucker trawls alone, these data are presented separately. For species with insufficient data, data from both trawls are combined in the figures. In most cases larvae, which usually have a different vertical distribution than adults, have been excluded from the distribution figures and the

TABLE 1.—Depth distribution, capture rates, and numbers of the most abundant cephalopod species captured by the Isaacs-Kidd midwater trawl. Day captures for *Pterygioteuthis giardi* are included in Figure 4. R = capture rate in numbers per 1,000 m^3 of water sampled. N = actual number captured. ND = no data.

	Day						Night							
	Abraliopsis sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Abraliopsis* sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Pterygioteuthis giardi*	
Depth (m)	R	N	R	N	R	N	R	N	R	N	R	N	R	N
0-50	ND	ND	ND	ND	ND	ND	5.4	14	15.2	39	1.5	4	5.8	15
50-100	ND	ND	ND	ND	ND	ND	17.9	52	62.1	180	6.5	19	7.9	23
100-150	ND	ND	ND	ND	ND	ND	3.2	8	23.3	57	7.3	18	2.0	5
150-200	0	0	0	0	0	0	5.2	14	14.1	38	15.9	43	2.2	6
200-250	0	0	0	0	0	0	1.0	1	0	0	3.1	3	0	0
250-300	ND	ND	ND	ND	ND	ND	1.0	1	1.0	1	6.5	6	4.3	4
300-400	3.0	4	2.3	3	6.9	9	0	0	0	0	0	0	0	0
400-500	10.9	14	42.3	54	14.1	18	4.9	3	4.9	3	4.9	3	0	0
500-600	7.4	9	72.2	87	20.7	25	3.4	2	6.9	4	5.1	3	0	0
600-700	22.8	26	8.7	10	14.9	17	0	0	1.4	1	0	0	0	0
700-800	1.0	2	5.3	10	3.2	6	2.8	3	0	0	0	0	0	0
800-900	3.6	3	8.5	7	1.2	1	0	0	0	0	0	0	0	0
900-1,000	2.1	2	1.0	1	2.1	2	0	0	0	0	0	0	0	0
1,000-1,100	1.5	1	20.1	13	1.5	1	0	0	0	0	5.4	1	0	0

TABLE 2.—Trawling time in minutes. Since trawls of two different sizes were used, a correction factor of 0.6 was applied to the trawling times of the Tucker trawl to compute the adjusted total trawling time. This factor represents the approximate difference in effective mouth areas of the two nets. Open tows = time of each tow was assigned to one depth. Opening-closing tows = time of each tow was apportioned among depth zones traversed by the trawl. IKMT = Isaacs-Kidd midwater trawl.

	Tucker trawl				IKMT		Total adjusted to IKMT	
	Open		Opening-closing		Open			
Depth (m)	Day	Night	Day	Night	Day	Night	Day	Night
0-50		1,091		939		2,562		3,780
50-100	180	1,112		614		2,897	108	3,932
100-150		781	27	591		2,442	16	3,265
150-200	144	530	84	870	130	2,689	267	3,529
200-250		536	186	320	177	944	289	1,458
250-300	146		31	871		911	106	1,434
300-350	180		203	514	452	605	682	913
350-400	180	180	460	407	839	552	1,223	904
400-500	360	502	1,529	1,413	1,276	605	2,409	1,754
500-600		376	1,748	927	1,204	577	2,253	1,359
600-700		133	1,683	1,420	1,139	714	2,149	1,646
700-800	313	220	1,638	838	1,862	1,052	3,033	1,687
800-900			1,244	519	820	179	1,566	490
900-1,000	180	30	709	184	917	179	1,450	307
1,000-1,100		182	464	64	646	182	924	330
1,100-1,200	195		230	156	180	195	435	289
1,200-1,300	200	300	380		180		528	180
1,300-1,400	10	256	234	98			146	212
1,400-1,500			67	106			40	64
1,500-1,600				30				18
1,600-1,700			8	38			5	23
1,700-1,800			104	267			62	160
1,800-1,900			84	228			50	137
1,900-2,000			48	28			29	17
2,000-2,100			15	27			9	16
2,100-2,200			72	29			43	17
2,200-2,300			43	33			26	20
2,300-2,400				8				5

text. Specimens captured during twilight periods, with a few exceptions, have also been excluded from the charts.

Species examined are listed in Table 3. Larvae or juveniles of several additional species were captured but are not included in this study. These are: *Tremoctopus violaceus, Argonauta* sp., *Cranchia scabra, Thysanoteuthis rhombus, Onykia* sp. One pelagic species reported from Hawaii by Berry (1914), *Iridoteuthis iris*, was not taken. This species belongs in the genus *Nectoteuthis* and probably lives in association with the ocean floor.[2]

Photosensitive vesicles of most species were sectioned. Material was fixed either in glutaraldehyde-osmium tetroxide or Bouin's solution and was embedded in Epon 812[3] or paraffin. All vesicles sectioned contained cells with photosensitive processes and, therefore, appeared to be functional. In only a few cases did the general histology of the organs add to our understanding of their function. As a result, histological details are not included for most species.

In order to quantify the size of vesicles, an attempt was made to obtain dry weights. Many types of vesicles proved difficult to remove and clean completely. Vesicles from a series of similar-sized *Pyroteuthis addolux*, which are easily removed, were weighed and found to vary by a factor of 1.5. Because of the large individual variations and inaccuracies due to difficulties in isolating many types of vesicles, this method of quantification was abandoned. As a result, camera lucida drawings of photosensitive vesicles provide the only measure of organ size: their relative size can be approximately determined by comparison with the brain size.

RESULTS

Pyroteuthis addolux Young 1972

Vertical Distribution

During the day, 39 specimens captured by the Tucker trawl indicate a vertical range for this

[2]Roper, C., and R. Young. Review of the Heteroteuthinae. Unpubl. manuscr.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.—Species of cephalopods considered.

Order Teuthoidea
- Family Enoploteuthidae
  - *Pyroteuthis addolux* Young 1972
  - *Pterygioteuthis microlampas* Berry 1913
  - *Pterygioteuthis giardi* Fischer 1895
  - *Abralia trigonura* Berry 1913
  - *Abralia astrosticta* Berry 1909
  - *Abraliopsis* sp. A, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. B, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. C, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. A, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. B, n.sp. being described by L. Burgess
  - *Thelidioteuthis alessandrinii* (Vérany 1851)
- Family Ommastrephidae
  - *Symplectoteuthis oualaniensis* (Lesson 1830)
  - *Hyaloteuthis pelagicus* (Bosc 1802)
  - *Nototodarus hawaiiensis* (Berry 1912)
- Family Histioteuthidae
  - *Histioteuthis dofleini* (Pfeffer 1912)
  - *Histioteuthis celetaria pacifica* (Voss 1962)
  - *Histioteuthis* sp. under study by N. Voss
- Family Neoteuthidae
  - *Neoteuthis* sp.
- Family Bathyteuthidae
  - *Bathyteuthis abyssicola* Hoyle 1885
- Family Ctenopterygiidae
  - *Ctenopteryx siculus* (Vérany 1851)
- Family Onychoteuthidae
  - *Onychoteuthis compacta* (Berry 1913)
- Family Octopoteuthidae
  - *Octopoteuthis nielseni* Robson 1948
- Family Cycloteuthidae
  - *Cycloteuthis serventyi* Joubin 1919
  - *Discoteuthis laciniosa* Young and Roper 1969
- Family Brachioteuthidae
  - *Brachioteuthis* sp.
- Family Chiroteuthidae
  - *Chiroteuthis* n.sp., being described by Roper and Young
  - *Chiroteuthis picteti* Joubin 1894
  - Chiroteuthidae n.gen., n.sp. being described by Roper and Young
  - *Planktoteuthis lippula* (Chun 1908)
  - *Grimalditeuthis bomplandi* (Vérany 1837)
- Family Mastigoteuthidae
  - *Mastigoteuthis famelica* (Berry 1909)
  - *Mastigoteuthis inermis* Rancurel 1972
- Family Joubiniteuthidae
  - *Joubiniteuthis portieri* (Joubin 1912)
- Family Cranchiidae
  - *Liocranchia valdiviae* (Chun 1906)
  - *Liocranchia reinhardti* (Steenstrup 1856)
  - *Leachia pacifica* (Issel 1908)
  - *Phasmatopsis fisheri* (Berry 1909)
  - *Taonius pavo* (LeSueur 1821)
  - Sandalops melancholicus Chun 1906
  - *Helicocranchia beebei* Robson 1948
  - *Bathothauma lyromma* Chun 1906

Order Octopoda
- Family Bolitaenidae
  - *Eledonella pygmaea* Verrill 1884
  - *Japetella diaphana* Hoyle 1885
- Family Amphitretidae
  - *Amphitretus pelagicus* Hoyle 1885
- Family Vitreledonnellidae
  - *Vitreledonnella richardi* Joubin 1918

Order Vampyromorpha
- Family Vampyroteuthidae
  - *Vampyroteuthis infernalis* Chun 1903

Order Sepioidea
- Family Sepiolidae
  - *Heteroteuthis hawaiiensis* (Berry 1909)

species of 375 to 510 m; most captures came from 450 to 500 m (Figure 1). IKMT data lumped into 100-m increments show most day captures between 400 and 700 m (Table 1). At night, 38 of the 41 specimens captured by the Tucker trawl indicate a vertical range of about 110 to 225 m; most specimens came from 150 to 200 m. Three specimens were captured during the night in opening-closing tows near their day habitat at depths between 360 and 480 m. Each of these three specimens was taken in a separate tow during a cruise in November 1972 within a few days of new moon. Although the upper 200 m was not sampled on this cruise, these captures indicate that at least part of

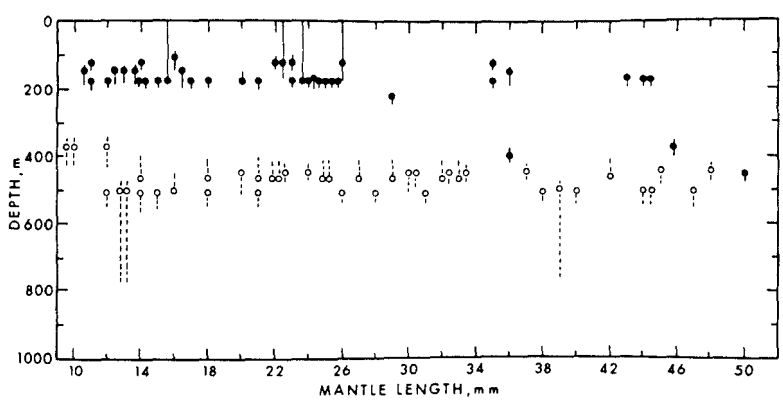

FIGURE 1.—Vertical distribution of *Pyroteuthis addolux*. Symbols for Figure 1 and subsequent figures: open circles represent day captures; closed circles represent night captures. A bar with a circle indicates an opening-closing tow with the bar representing the depth range of the tow and the circle the most likely depth of the capture (the modal depth, or if no clear mode is present, the midpoint of the vertical range of the tow). A circle without a bar indicates a capture in an open tow. A bar without an associated symbol indicates an open oblique tow. Such bars do not always intersect the zero depth line as some gradual oblique tows were made between specific depths. Solid bars represent night captures. Dashed bars represent day captures. A small dot represents a presumed contaminant.

the population was not migrating during this period. IKMT data lumped into 50-m increments show that most night captures were made between 50 and 200 m with peak catches between 150 and 200 m.

Photosensitive Vesicles (Figure 2A)

The organs are very similar to those described by R. E. Young (1977) in *Pterygioteuthis microlampas*. *Pyroteuthis addolux* has two sets of organs. The dorsal organs (the more dorsal set) lie embedded in the posterodorsal wall of the cephalic cartilage and adjacent to the optic lobes of the brain. Each ventral organ lies deeply embedded in the posteroventral surface of the cephalic cartilage. Except for a thin medial extension on each ventral organ, all organs are thick, compact, and approximately circular to square in outline. The histological structure of the dorsal and ventral organs is similar. The integument adjacent to both the dorsal and ventral organs lacks pigment and thereby forms distinctive "windows" for the passage of light.

Nerves from both dorsal and ventral organs enter the peduncle complex of the brain and their fibers disperse in the base of the peduncle lobe near its broad junction with the olfactory lobe.

Pterygioteuthis microlampas Berry 1913

Vertical Distribution (Figure 3)

The vertical distribution has been described by R. E. Young (1977). During the day, 48 specimens captured with the Tucker trawl indicate a depth range of 450 to 575 m; 85% of the specimens were taken between 450 and 500 m. IKMT data lumped into 100-m increments (Table 1) show most day captures between 400 and 600 m. At night 56 specimens taken by the Tucker trawl indicate a depth range of 25 to 180 m; nearly 85% of the captures were made between 50 and 105 m. IKMT data lumped into 50-m increments indicate a range of 0 to 200 m with a strong peak in the 50- to 100-m depth zone. The night distribution was not affected by moonlight (R. E. Young 1977).

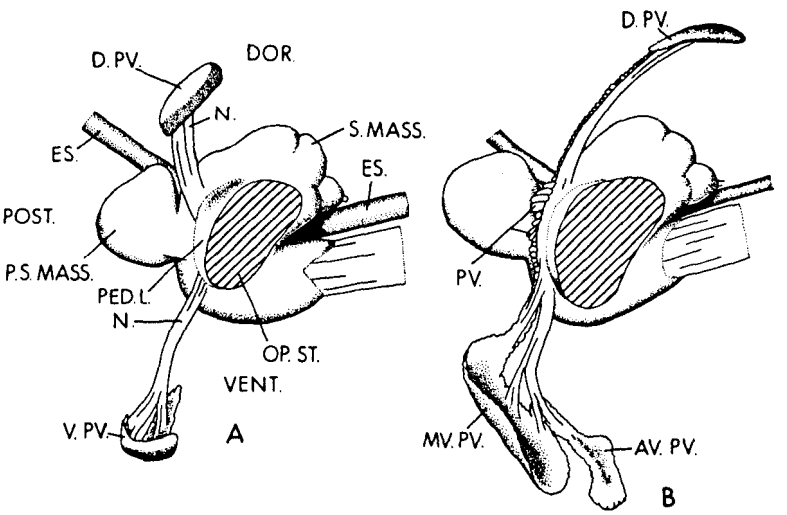

FIGURE 2.—A. Photosensitive vesicles of *Pyroteuthis addolux*. This illustration and most subsequent drawings show a side view of the brain. The optic stalk has been cut (as indicated by cross-hatching) and the optic lobe removed. The esophagus can be seen passing through the brain. Three major subdivisions of the brain are apparent (i.e., the supraesophageal mass, the posterior subesophageal mass, and the middle subesophageal mass.) A large nerve tract which extends anteriorly to the anterior subesophageal mass was cut (indicated by dotted line) and the latter portion of the brain is not shown. B. Photosensitive vesicles of *Abraliopsis* sp. B. Abbreviations for Figure 2 and subsequent figures of photosensitive vesicles: AV. PV.—Anteroventral photosensitive vesicles; C. PV.—central photosensitive vesicles; DOR.—dorsal; D. PV.—dorsal photosensitive vesicles; ES.—esophagus; GILL—gill; H. RET. M.—head retractor muscles; INT.—intestine; M. S. MASS—middle subesophageal mass of the brain; MV. PV.—midventral photosensitive vesicles; N.—nerve; OP. ST.—optic stalk; PED. L.—peduncle lobe; PIG. S.—pigment screen; POST.—posterior; P. PV.—posterior photosensitive vesicles; P. S. MASS—posterior subesophageal mass of the brain; PV.—Photosensitive vesicles; V. PV.—ventral photosensitive vesicles; S. MASS—supraesophageal mass of the brain; VENT.—ventral.

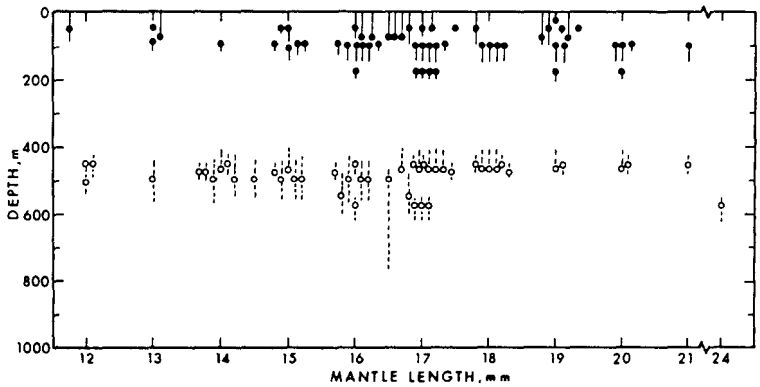

FIGURE 3.—Vertical distribution of *Pterygioteuthis microlampas*. From R. E. Young (1977). Symbols as in Figure 1.

Photosensitive Vesicles

The organs have been described by R.E. Young (1977). They are essentially the same as in *Pyroteuthis addolux*.

Pterygioteuthis giardi Fischer 1895

Vertical Distribution (Figure 4)

During the day 30 specimens captured from both trawls indicate a depth range from about 390 to 525 m; over 90% of the captures were made between 390 and 450 m. One IKMT tow captured eight badly damaged specimens at 630 m, well below their zone of maximum abundance. The previous tow had captured six specimens at 390 m that were in excellent condition; specimens from the deeper tow probably are contaminants. The depth distribution of this species may be biased by the relatively low sampling effort between 350 and 400 m.

At night, 39 captures with the Tucker trawl indicate a depth range of 15 to 180 m; over 75% of the specimens came from 15 to 50 m. IKMT data lumped into 50-m increments (Table 1) show the maximum abundance at depths of 0 to 100 m.

Photosensitive Vesicles

The organs are essentially the same as in *Pyroteuthis addolux*.

Abralia trigonura Berry 1913

Vertical Distribution (Figure 5)

Fifty specimens were captured by both trawls. Excluding presumed contaminants, the day captures were made between 390 and 650 m with nearly 80% between 450 and 560 m. At night captures were made between 30 and 200 m with over 75% between 50 and 100 m.

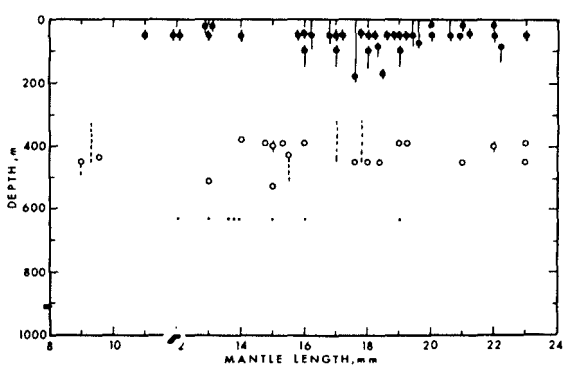

FIGURE 4.—Vertical distribution of *Pterygioteuthis giardi*. Symbols as in Figure 1.

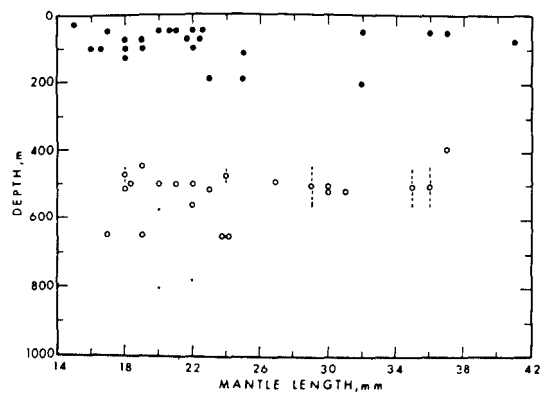

FIGURE 5.—Vertical distribution of *Abralia trigonura*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 6)

The arrangement of organs is similar to *Abraliopsis* sp. described by Young (1973). Four sets of organs are present; all lie adjacent to the cephalic cartilage. One set is located dorsally, one posteriorly, and two ventrally. Each dorsal organ is situated in a concavity of the cephalic cartilage at the posterodorsal edge of the head. The organ is compact, dorsoventrally flattened and circular to triangular in outline. The posterior organs are located on the posterior surfaces of the optic lobes. Each is approximately elliptical and very flat. The posterior organs have a strong yellow pigment which does not fade after fixation. Other organs contain an orange pigment that is lost after fixation. The posterior organs lie immediately anterior and lateral to the opaque liver and directly anterior to the attachment zone of the transparent head retractor muscles (Figure 6B). The ventral organs on each side consist of two, narrowly joined, flattened lobes. One of these, the anteroventral lobe, is located somewhat anterior and medial to the other. The anteroventral lobe has its medial and anterior ends in a deep depression of the cephalic cartilage. The anteromedial edge of each lobe nearly makes contact with its counterpart of the opposite side. The more posterior of the two lobes, the midventral lobe, lies between the ventral surface of the optic lobe and the cephalic cartilage.

Circular windows, similar to those described in *Abraliopsis* sp. (Young 1973), and characterized by a reduced number of chromatophores, are present above each dorsal organ. A large ventral window, totally lacking chromatophores, lies on the ventral surface of the head above the funnel and below the ventral vesicles.

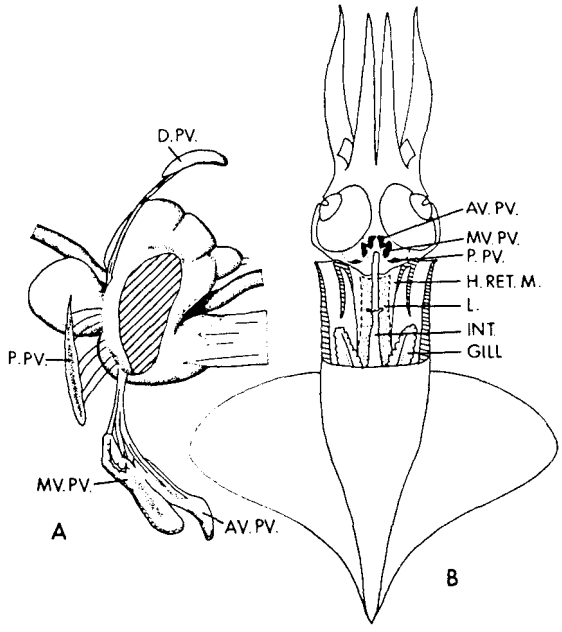

FIGURE 6.—A. Photosensitive vesicles of *Abralia trigonura*. B. Ventral view of *A. trigonura* with portion of mantle removed. This illustration shows the relationship between the posterior photosensitive vesicles, the opaque liver (L), and the mantle cavity. Abbreviations as in Figure 2.

Abralia astrosticta Berry 1909

Vertical Distribution

No specimens were captured during the present program. However, one specimen was taken in a gill net set overnight by T. Clarke on the bottom in 180 m. The National Marine Fisheries Service, NOAA, has captured 44 juveniles (7-38 mm ML (Mantle length)) in pelagic trawls between 10 and 130 m at night and 10 adults in a benthic shrimp trawl at 110 m at night near Hawaii. The type was captured in a bottom dredge between 354 and 650 m, presumably during the day. Roper and Young (1975) indicated that this animal lives near the ocean floor even when migrating.

Photosensitive Vesicles

The organs and associated windows are basically the same as in *A. trigonura*.

Abraliopsis sp. A

Vertical Distribution (Figure 7)

Sixty-seven specimens were captured. Exclud-

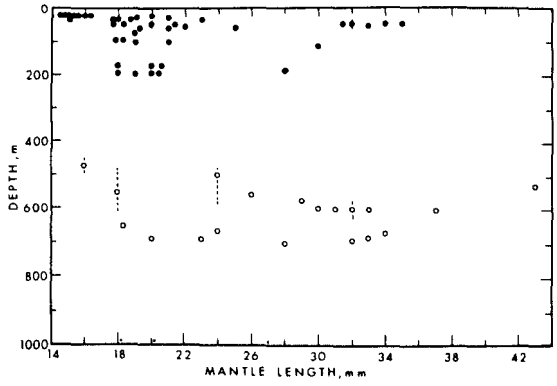

FIGURE 7.—Vertical distribution of *Abraliopsis* sp. A. Symbols as in Figure 1.

ing presumed contaminants, specimens captured during the day came from depths of about 475 to 700 m; 80% were taken between 550 and 700 m. At night, captures were made between about 20 and 200 m; nearly 80% were taken in the upper 100 m.

Photosensitive Vesicles

The organs and associated windows have been described in detail by Young (1973); they are similar to those of *Abralia trigonura*.

Abraliopsis sp. B

Vertical Distribution (Figure 8)

During the day, 23 specimens taken by the Tucker trawl indicate a depth range of 500 to 650 m; most captures came from 500 to 600 m. IKMT data lumped into 100-m increments indicate most specimens came from 400 to 700 m.

At night, 19 specimens from the Tucker trawl probably came from depths between 50 and 100 m. IKMT data lumped into 50-m increments show a strong peak in the 50- to 100-m interval. A few IKMT captures were made as shallow as 15 m.

Photosensitive Vesicles (Figure 2B)

The dorsal and anteroventral organs are similar to other species of *Abraliopsis* and *Abralia*. The posterior lobes, however, are absent, and the midventral lobes are enlarged and extended dorsally. In addition, a thin string of vesicles extends from each midventral lobe dorsally between the brain and the optic lobe to join with the dorsal lobe. The structure of this string is slightly variable, and in some specimens the vesicles found about at mid-brain level are slightly enlarged and elongate (Figure 2B). The yellow pigment characteristic of the posterior lobes in related species does not occur in any of the lobes of this species.

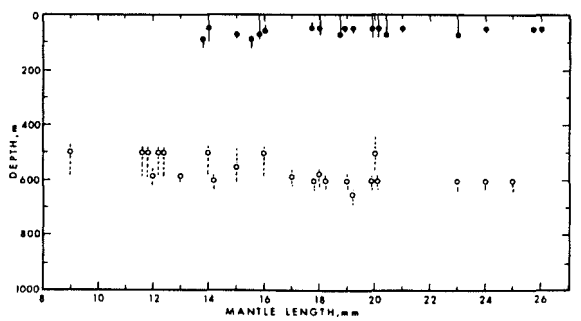

FIGURE 8.—Vertical distribution of *Abraliopsis* sp. B. Symbols as in Figure 1.

Abraliopsis sp. C

Vertical Distribution (Figure 9A)

Only 12 specimens were captured. During the day, five specimens were taken between 500 and 600 m. At night, all of the captures were made in the upper 100m.

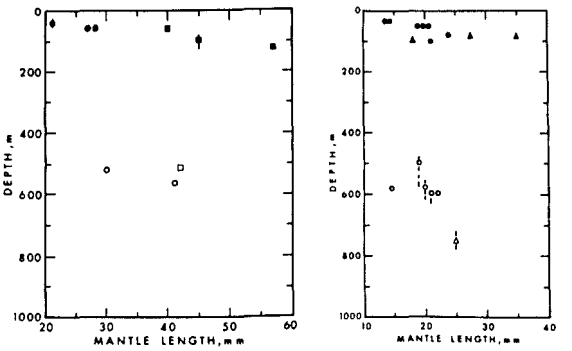

FIGURE 9.—A. Vertical distribution of *Enoploteuthis* sp. A (circles) and *Enoploteuthis* sp. B (squares). B. Vertical distribution of *Abraliopsis* sp. C (circles) and *Thelidioteuthis allesandrinii* (triangles). Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *Abralia trigonura* and *Abraliopsis* sp. A except that the posterior lobe is smaller, slightly more medially located, and continuous with the midventral organ. This latter connection, however, does not have the yellow pigment that the posterior organ possesses. Also, a few scattered vesicles lie on the posterior margin of the nerve from the dorsal organ.

Enoploteuthis sp. A

Vertical Distribution (Figure 9B)

During the day, two captures were made between 500 and 600 m; and at night, three captures were made in the upper 100 m.

Photosensitive Vesicles (Figure 10A)

The organs are similar to *Abralia trigonura*

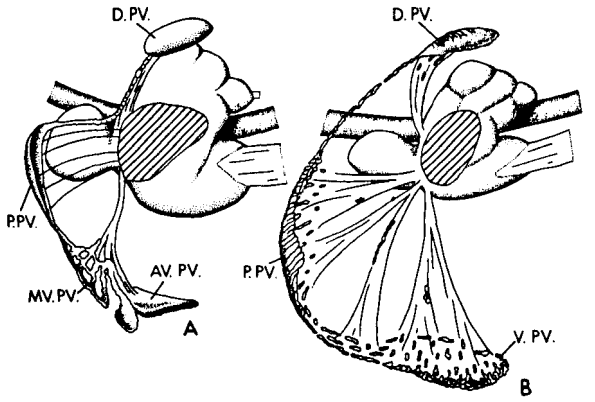

FIGURE 10.—A. Photosensitive vesicles of *Enoploteuthis* sp. A. B. Photosensitive vesicles of *Thelidioteuthis alessandrinii*. Abbreviations as in Figure 2.

with the following exceptions. The midventral organ has a more irregular shape, is less compact, and has a narrow connection with the posterior organ. The posterior organ is continuous with the dorsal organ via a strand of vesicles that extends over the optic lobe. Except for a short segment adjacent to the dorsal organ, this strand contains yellow pigment as does the posterior lobe.

Enoploteuthis sp. B

Vertical Distribution (Figure 9B)

One specimen was captured during the day at 515 m and three were taken at night between 50 and 150 m.

Photosensitive Vesicles

The vesicles are the same as those of *Enoploteuthis* sp. A except for some differences in the posterior organ. The posterior organ in *Enoploteuthis* sp. B is more elongate, more medially located on the optic lobe, and lacks yellow pigment.

Thelidioteuthis alesandrinii (Vérany 1851)

Vertical Distribution (Figure 9A)

During the day, one specimen was taken in an opening-closing tow between 720 and 780 m. At night, three specimens were taken in open tows between 80 and 100 m.

Photosensitive Vesicles (Figure 10B)

Three sets of organs, dorsal, posterior, and ventral, consist primarily of a loose association of variously shaped, mostly independent vesicles (Young 1977). The organs are broad, flat structures, with the greatest concentration of vesicles along the lateral margins of the organs. The organs lack yellow pigment.

Family Ommastrephidae

Symplectoteuthis oualaniensis (Lesson 1830)

Vertical Distribution

Except for larvae, only one specimen was captured in the midwater trawls. This specimen was taken at night by the IKMT which fished at 100 m. This fast-swimming squid normally avoids our trawls. Members of this species are commonly seen at the surface at night around the night-light and a number have been dipnetted. Little is known, however, of their day distribution, although Young (1975b) had assembled evidence which indicates that they live in the upper few hundred meters but may descend on occasion to great depths.

Photosensitive Vesicles (Figure 11A)

Three sets of organs are present: a dorsal, central, and ventral set. The ventral organ lies within the cephalic cartilage at the posterior end of the head and immediately above the posterolateral portion of the funnel. It consists of a series of flat,

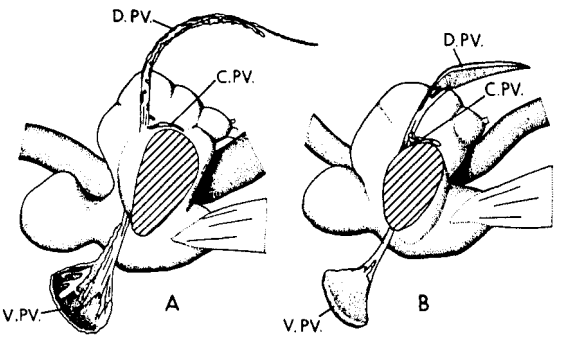

FIGURE 11.—A. Photosensitive vesicles of *Symplecoteuthis oualaniensis*. B. Photosensitive vesicles of *Hyaloteuthis pelagicus*. Abbreviations as in Figure 2.

elongate vesicles that are most numerous at its ventral end. The central organ consists of a few small, flat, elongate vesicles located on the dorsal surface of the optic stalk. The vesicles of the dorsal organ are scattered along a broad arching nerve that extends from the peduncle lobe dorsally then anteriorly along the dorsomedial margin of the optic lobe. The vesicles are flat and irregularly shaped.

Hyaloteuthis pelagicus (Bosc 1802)

Vertical Distribution

The single specimen captured was taken in an opening-closing tow between 1,700 and 2,200 m during the day. The specimen was a gravid female: the ovary was packed with mature eggs, the nidamental and oviducal glands were greatly enlarged, and numerous discharged spermatophores were attached to the lips surrounding the mouth. Specimens in similar condition as well as immature specimens have been captured frequently at a depth of about 100 m at night by the National Marine Fisheries Service, NOAA, in Honolulu using a large Cobb trawl. *Hyaloteuthis pelagicus* typically avoids our midwater trawls. The single day capture demonstrates that this species is capable of descending to great depths. Unfortunately, nothing is known of its normal day habitat.

Photosensitive Vesicles (Figure 11B)

Three sets of organs similar to those of *S. oualaniensis* are present. A small central organ lies just dorsal to the optic stalk and consists of a relatively small number of rather large vesicles. Each dorsal organ lies above the dorsomedial side of the optic lobe and is a large, compact triangular organ with irregularly shaped vesicles. The ventral organ is a flat, compact, oval organ which abuts against the cephalic cartilage above the lateral base of the funnel.

Nototodarus hawaiiensis (Berry 1912)

Vertical Distribution

No specimens have been taken in our midwater trawls; however, 63 specimens were captured in 40-ft shrimp trawls by the National Marine Fisheries Service. Specimens captured during the day came from depths of 230 to 710 m, although only a single capture was made below 420 m. Night captures range from 110 to 410 m. During the late summer and early fall, this species is commonly taken by dip net or near-surface jig at night off the island of Hawaii.

Photosensitive Vesicles (Figure 12A)

Three sets of organs are present similar to those in *S. oualaniensis* and *H. pelagicus*. The central organ is slightly larger than that of *S. oualaniensis* but is positioned similarly. The dorsal organ consists of a flat strip of vesicles that extends from the central organ dorsally to the cephalic cartilage. The margins of this organ are irregular, and thin strings of vesicles extend away from the organ at various places. Where the dorsal organ connects with the central organ, the two can be distinguished by the sizes of their individual vesicles: the small central organ consists of relatively few large vesicles, while the dorsal organ consists of numerous small vesicles. The ventral organ is compact, flattened, and somewhat club-shaped. It occupies about the same position as the corresponding organs in *S. oualaniensis* and *H. pelagicus*.

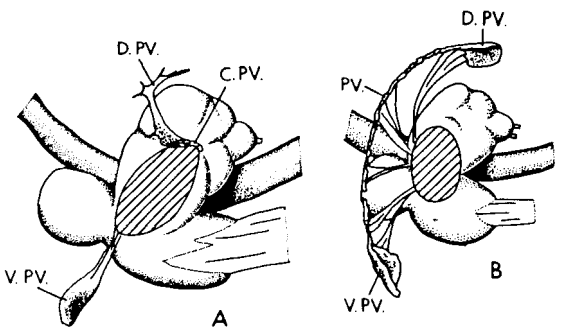

FIGURE 12.—A. Photosensitive vesicles of *Nototodarus hawaiiensis*. B. Photosensitive vesicles of *Histioteuthis dofleini*. Abbreviations as in Figure 2.

Family Histioteuthidae

Histioteuthis dofleini (Pfeffer 1912)

Vertical Distribution (Figure 13)

The vertical distribution of this species has been discussed by Young (1975c). The vertical range is 375 to 850 m during the day; over 80% of the captures came from depths of 500 to 700 m. At

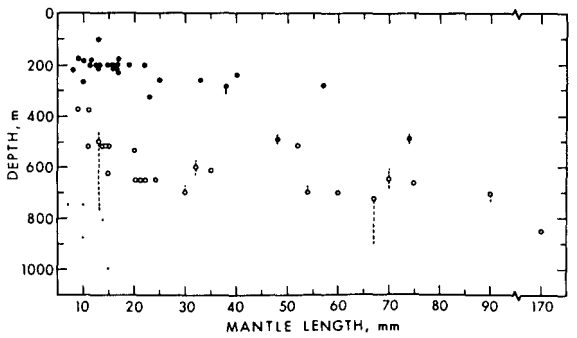

FIGURE 13.—Vertical distribution of *Histioteuthis dofleini*. From Young (1975c). Symbols as in Figure 1.

night, the range is 100 to 500 m; over 85% of the captures came from depths of 150 to 300 m. During both the day and night, larger individuals tend to be found at slightly greater depths.

Photosensitive Vesicles (Figure 12B)

Histioteuthis dofleini has two sets of vesicles, a dorsal and a ventral set, joined by a narrow strand of vesicles. The dorsal and ventral organs are flat and approximately the same size. The dorsal organs lie dorsal to the optic lobes, and the ventral organs lie above the lateral bases of the funnel (R. E. Young 1977).

Histioteuthis celetaria pacifica (Voss 1962)

Vertical Distribution (Figure 14A)

A single day capture came from 550 m. Four night captures came from depths of about 250 to 400 m.

Photosensitive Vesicles

The vesicles are similar to those of *H. dofleini* except that the dorsal and ventral organs are more compact.

Histioteuthis sp.

Vertical Distribution (Figure 14A)

Two day captures came from depths of 575 and 665 m, and four night captures were made between depths of 165 and 275 m.

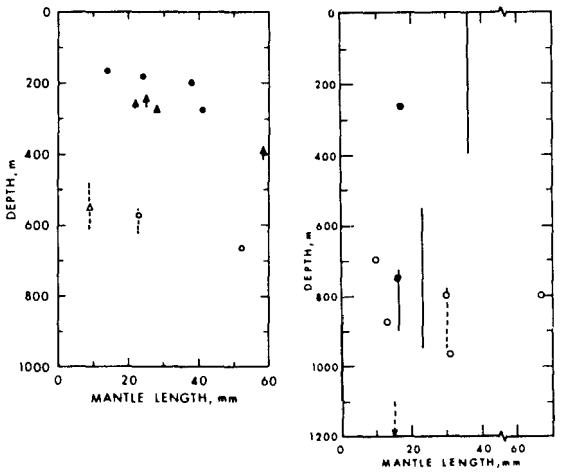

FIGURE 14.—A. Vertical distribution of *Histioteuthis celetaria pacifica* (triangles) and *Histioteuthis* sp. (circles). B. Vertical distribution of *Bathyteuthis abyssicola*. Symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *H. dofleini*.

Neoteuthis sp.

Vertical Distribution

A single small specimen was taken in an IKMT tow that fished between the surface and 350 m at night. Roper and Young (1975) reported nine specimens from the Atlantic Ocean taken in open tows between 1,300 and 2,000 m at night and one specimen taken in a closing net at 900 m at night.

Photosensitive Vesicles (Figure 15A)

Neoteuthis sp. has only one set of organs. Each organ consists of a small grapelike cluster of globular vesicles arising from the medioposterior surface of the peduncle lobe and extending ventrally below the optic stalk.

Bathyteuthis abyssicola Hoyle 1885

Vertical Distribution (Figure 14B)

Five of six specimens captured during the day were taken between 700 and 975 m. The remaining specimen was taken in an oblique IKMT tow that fished between 1,100 and 1,900 m. At night, two specimens were taken in the upper 400 m, a

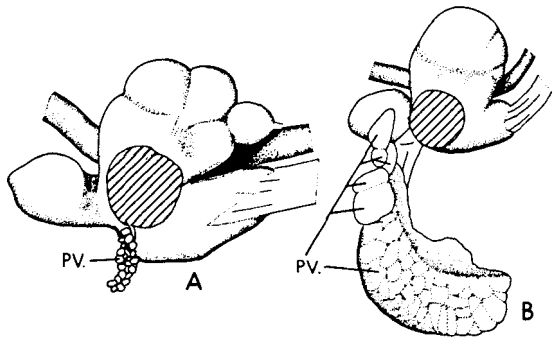

FIGURE 15.—A. Photosensitive vesicles of *Neoteuthis* sp. B. Photosensitive vesicles of *Bathyteuthis abyssicola*. Abbreviations as in Figure 2.

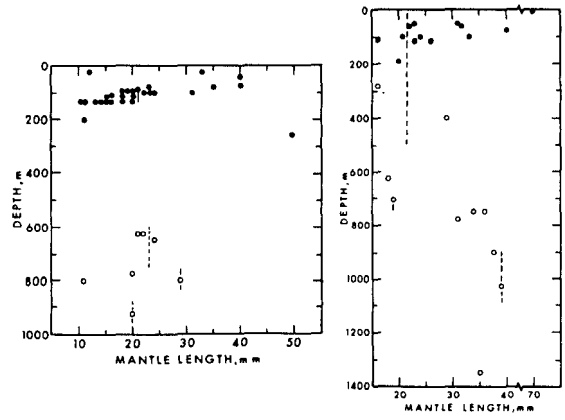

FIGURE 16.—A. Vertical distribution of *Ctenopteryx siculus*. B. Vertical distribution of *Onychoteuthis compacta*. Symbols as in Figure 1.

third was taken in an opening-closing tow at about 750 m, and the fourth in an open oblique tow that fished between 550 and 950 m.

Photosensitive Vesicles (Figure 15B)

The organs have been described in detail by Young (1972a). One set of very large organs is present. Each organ is located adjacent to the posteroventral surface of the eye and above the posterolateral edge of the funnel. Posterior to the organ the skin is only lightly pigmented and forms a "window."

Family Ctenopterygiidae

Ctenopteryx siculus (Vérany 1851)

Vertical Distribution (Figure 16A)

Seven of eight specimens captured during the day came from depths of about 625 to 800 m; the other specimen came from about 925 m. At night 28 specimens were captured between depths of 25 to 260 m; over 80% of the specimens were taken between 50 and 150 m.

Photosensitive Vesicles (Figure 17A)

Ctenopteryx sicula has a single pair of large and highly organized organs. Each organ consists of a single elongate and flattened but curved vesicle. Each organ extends from the posterior end of the supraesophageal mass, beneath the optic stalk, and anterior to the middle subesophageal mass where it joins with its counterpart from the opposite side. The organ, therefore, occupies a groove between the central brain and the optic lobes. The area where the two vesicles join lies just above the funnel approximately at the point where the funnel adductor muscles (bridles) attach to the cephalic cartilage. An iridophore sheath is continuous and encloses both organs in this region, but the vesicles do not actually fuse. That is, the lumen of each vesicle remains separate. The vesicles broaden slightly at their dorsal end and in the region of the junction. The anterodorsal walls of each vesicle are convex and lined with dense layers of iridophores; light enters through the

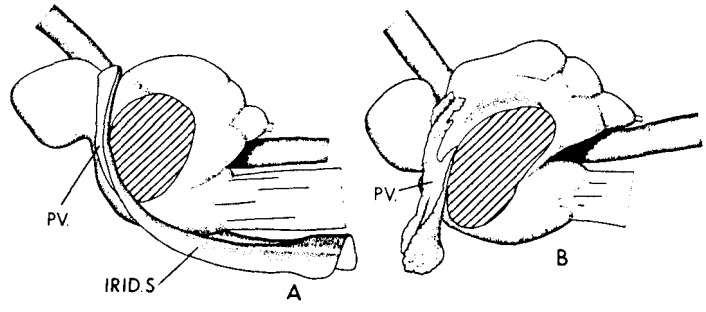

FIGURE 17.—A. Photosensitive vesicles of *Ctenopteryx siculus*. B. Photosensitive vesicles of *Onychoteuthis compacta*. IRID. S.—Iridophore screen. Otherwise, abbreviations as in Figure 2.

posteroventral surfaces. The sensory processes within the vesicles are highly organized, particularly in the ventral portions. The wall of the organ is not particularly thick, and usually has two irregular layers of sensory-cell bodies. The sensory processes arise from all sides of the vesicles; they are straight, parallel, and fill the lumen in the ventral parts of the organ. The sensory processes are about 30 to 50 μm long and lack a detectable core. The dorsal end of the organ lacks the iridophore sheath and has a slightly convoluted wall; the sensory processes are somewhat more widely spaced and do not fill the lumen of the vesicle.

Family Onychoteuthidae

Onychoteuthis compacta (Berry 1913)

Vertical Distribution (Figure 16B)

Twenty-five specimens were captured. Eleven specimens taken during the day came from depths of 240 to 1,350 m. At night, 12 of 14 captures were made between the surface (dip net) and 115 m. The two remaining captures came from depths of 190 and 310 m.

Photosensitive Vesicles (Figure 17B)

Onychoteuthis compacta has a single set of organs. Each organ consists of a large number of small, tightly packed vesicles. Each organ is located on the posterior edge of the optic stalk and extends ventrally and slightly laterally below the central brain along the medial side of the optic lobe. The ventrolateral portion of the vesicle lies directly posterior to the side of the liver and just medial to the head retractor muscles and immediately above the funnel.

Family Octopoteuthidae

Octopoteuthis nielseni Robson 1948

Vertical Distribution (Figure 18A)

Three specimens captured during the day came from depths of about 650 to 765 m. The six night captures came from depths between 100 and 200 m.

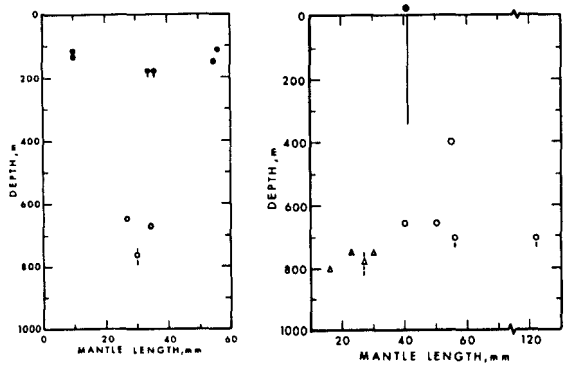

FIGURE 18.—A. Vertical distribution of *Octopoteuthis nielseni*. B. Vertical distribution of *Cycloteuthis serventyi* (triangles) and *Discoteuthis laciniosa* (circles). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 19A)

Two sets of organs are present. A compact ventral organ lies embedded in the thick cephalic cartilage at the anterolateral edge of the statocyst and just medial to the insertion of the head retractor muscles. This organ consists of large, globular, independent vesicles tightly packed together. A series of narrow, very elongate vesicles lie along the nerves from the organ. The central organ lies on the posterior surface of the optic stalk adjacent to the peduncle complex. This large and rather irregularly shaped organ consists of numerous small vesicles.

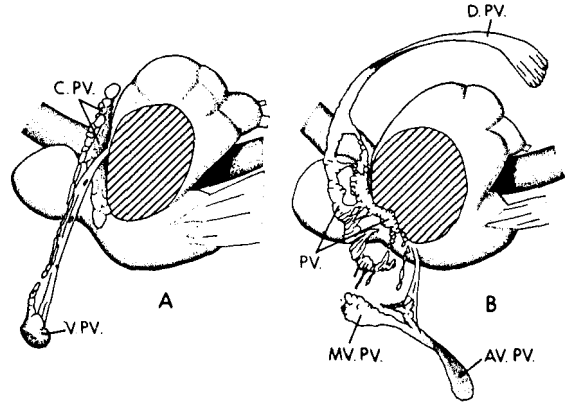

FIGURE 19.—A. Photosensitive vesicles of *Octopoteuthis nielseni*. Photosensitive vesicles of *Cycloteuthis serventyi*. Abbreviations as in Figure 2.

Family Cycloteuthidae

Cycloteuthis serventyi Joubin 1919

Vertical Distribution (Figure 18B)

Three specimens were taken between 750 and 800 m during the day. The single night capture came from an IKMT that fished at 750 m; however, the specimen may be a contaminant, as Roper and Young (1975) listed most of the known night captures of this species from the Atlantic in the upper 200 m.

Photosensitive Vesicles (Figure 19B)

The arrangement of vesicles is complex. On each side of the head, two flattened lobes are located ventral and lateral to the central brain in approximately the positions of the anteroventral and midventral lobes of the *Abraliinae*. The midventral lobe sometimes connects to a complex series of vesicles extending dorsally. These latter vesicles consist of two series: a more posterior series of irregular flattened vesicles lying on the posteromedial surface of the optic lobe; and a thicker, irregular, and rather extensive series of vesicles lying between the optic lobe and peduncle complex. These two series interconnect at various points. At about the level of the optic gland, a thin dorsal organ extends up the medial wall of each optic lobe and onto its anterodorsal surface. This terminal portion gradually widens but remains thin.

Discoteuthis laciniosa Young and Roper 1969

Vertical Distribution (Figure 18B)

Five specimens were taken during the day between 400 and 700 m, although the shallowest capture came from a tow that dipped briefly to 480 m. At night, a single specimen was taken in an oblique tow from the surface to 350 m.

Photosensitive Vesicles (Figure 20A)

The arrangement of vesicles is complex. A broad, flat, irregular ventral lobe is located between the posteroventral surface of the optic lobe and the cephalic cartilage, and opposite the insertion of the head retractor muscles. The broad, flat nerve passing to this lobe bears a series of often isolated vesicles or irregular strands of vesicles which, nearer the brain, join a single, somewhat flattened cord. This central organ extends dorsally and expands somewhat near the optic gland. Although this general pattern holds between specimens, considerable variation in the size of various parts of the central organ occurs.

Family Brachioteuthidae

Brachioteuthis sp.

Vertical Distribution (Figure 21)

Three specimens were captured during the day between 800 and 975 m. Only the mantle of a fourth specimen was present in a day tow at 450 m. The previous tow fished at 900 m and captured one of the other three specimens; the shallow capture is probably a contaminant. Seven of the eight specimens captured at night were taken between 30 and 235 m. The remaining specimen was taken at 1,125 m in an open tow and was a gravid female with sperm masses embedded in the buccal membrane.

Photosensitive Vesicles (Figure 20B)

A single set of organs is present. Each organ is situated on the posterior margin of the optic stalk

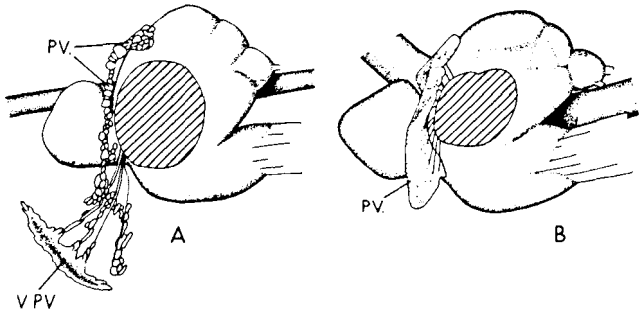

FIGURE 20.—A. Photosensitive vesicles of *Discoteuthis laciniosa*. B. Photosensitive vesicles of *Brachioteuthis* sp. Abbreviations as in Figure 2.

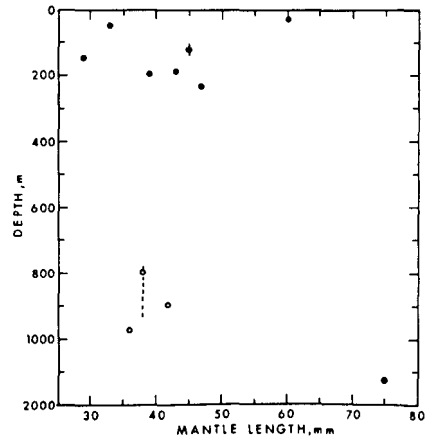

FIGURE 21.—Vertical distribution of *Brachioteuthis* sp. Symbols as in Figure 1.

and extends from the optic gland ventrally and laterally to the level of the ventral surface of the central brain. Each organ consists of numerous small tightly packed vesicles.

Family Chiroteuthidae

Chiroteuthis sp.

Vertical Distribution (Figure 22A)

Three specimens captured during the day were taken between 700 and 800 m. At night, eight specimens were captured between 15 and 750 m; however, six of these came from the upper 200 m.

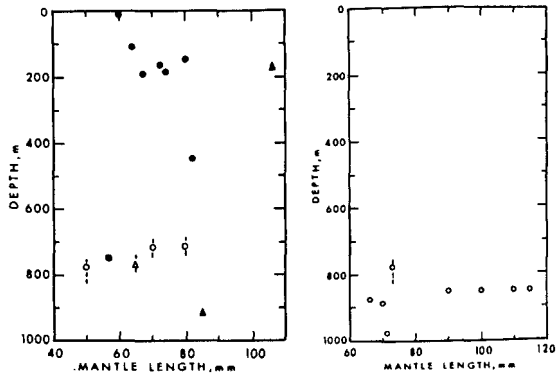

FIGURE 22.—A. Vertical distribution of *Chiroteuthis* sp. (circles) and *Chiroteuthis picteti* (triangles). B. Vertical distribution of Chiroteuthidae gen. sp. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 23A)

One set of small organs is present. Each organ arises on the posterior margin of the optic stalk and extends from the optic gland ventrally to about the level of the ventral surface of the central brain. The organ consists of many small, tightly packed vesicles. Growth of the vesicles from the juvenile stage on is allometric. While the size of each organ increases slightly, the number of component vesicles decreases.

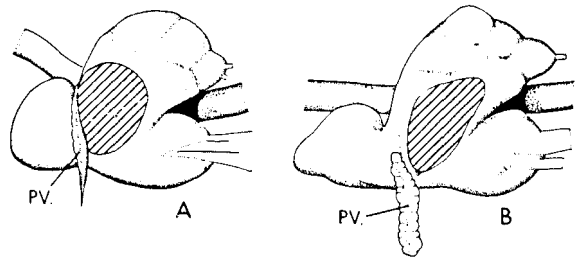

FIGURE 23.—A. Photosensitive vesicles of *Chiroteuthis* sp. B. Photosensitive vesicles of Chiroteuthidae gen. sp. Abbreviations as in Figure 2.

Chiroteuthis picteti Joubin 1894

Vertical distribution (Figure 22A)

Two day captures were made between 750 and 950 m, and a single night capture was made at 175 m.

Photosensitive Vesicles

The organs are essentially the same as in large specimens of *Chiroteuthis* sp. A.

Chiroteuthidae Gen. Sp.

Vertical Distribution (Figure 22B)

All eight specimens of this species were captured during the day between 775 and 975 m.

Photosensitive Vesicles (Figure 23B)

The organs are very similar to those in *Chiroteuthis* spp. One set is present. Each organ consists of small circular vesicles tightly packed into a well-defined organ that attaches to the posteroventral margin of the optic stalk.

Planktoteuthis lippula (Chun 1908)

Vertical Distribution (Figure 24)

Eighteen specimens were captured. Two captures between 200 and 300 m are young animals that probably had not descended to the adult depths. With the exception of a night capture at about 625 m, the remaining animals all came from depths of over 700 m. Among these deeper captures, there is an indication of ontogenetic descent. The largest specimens were captured in an oblique IKMT tow between 1,100 and 1,900 m.

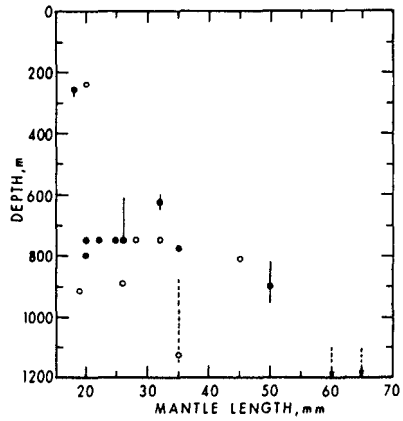

FIGURE 24.—Vertical distribution of *Planktoteuthis lippula*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25A)

One set of small organs is present. Each organ is attached to the ventral edge of the optic stalk and consists of a few globular vesicles.

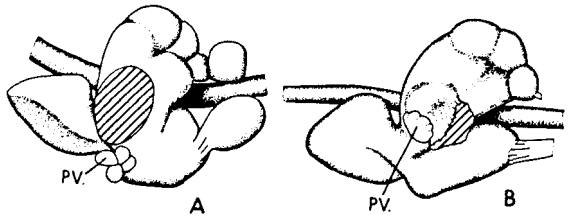

FIGURE 25.—A. Photosensitive vesicles of *Planktoteuthis lippula*. B. Photosensitive vesicles of *Grimalditeuthis bomplandi*. Abbreviations as in Figure 2.

Grimalditeuthis bomplandi (Vérany 1837)

Vertical Distribution (Figure 26A)

Three small specimens were taken at night in the upper 350 m and probably are individuals that had not descended from the larval depths. The larger specimens were all captured during the day between 750 and 1,275 m. The two largest specimens were the two deepest captures.

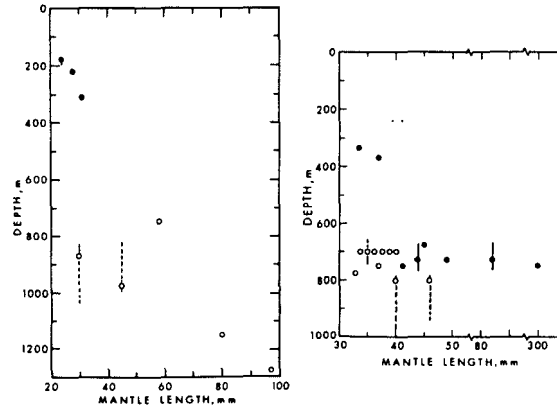

FIGURE 26.—A. Vertical distribution of *Grimalditeuthis bomplandi*. B. Vertical distribution of *Mastigoteuthis famelica*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25B)

One set of organs is present. Each organ consists of a small circular cluster of vesicles attached to the posteroventral margin of the optic stalk.

Family Mastigoteuthidae

Mastigoteuthis famelica (Berry 1909)

Vertical Distribution (Figure 26B)

Excluding contaminants, 16 of 18 specimens were taken between 675 and 800 m, both day and night. In addition, three specimens were probably contaminants. Two of these are assigned to a trawl that fished at 240 m during the day. These were probably captured during the previous tow at 700 m, which contained three specimens. Two shallow night captures of small animals may indicate that some of the population moves upward at night. However, since specimens of 41 mm ML or less are not far past the larval condition, these two specimens may represent animals in transit from the larval habitat.

Photosensitive Vesicles (Figure 27A)

Mastigoteuthis famelica has two sets of organs.

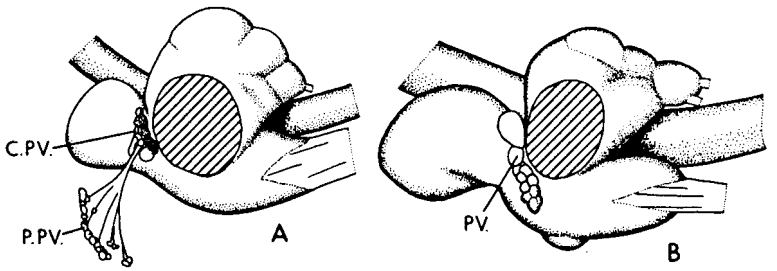

FIGURE 27.—A. Photosensitive vesicles of *Mastigoteuthis famelica*. B. Photosensitive vesicles of *Joubiniteuthis portieri*. Abbreviations as in Figure 2.

The central organs are located on the posterior margin of the optic stalk and consist of a dozen or so independent spherical vesicles. The posterior organs lie on the posterolateral surfaces of the optic lobes opposite the lateral attachment of the head retractor muscles. Each organ consists of a string of several layers of circular or oval vesicles. A few scattered vesicles occasionally occur along the nerves passing from the posterior organ.

Mastigoteuthis inermis Rancurel 1972

Vertical Distribution (Figure 28)

Fifteen specimens were captured during the day at depths of 675 to 870 m; most came from depths of about 700 to 800 m. Ten specimens captured at night came from depths of 255 to 725 m with most specimens being taken between 250 and 450 m.

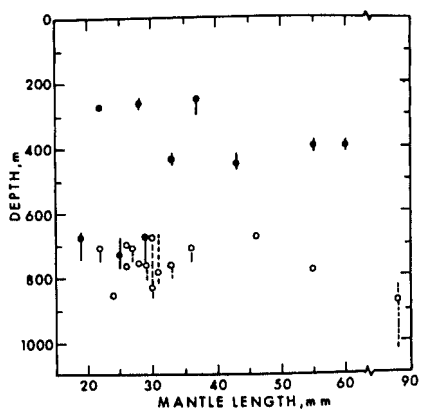

FIGURE 28.—Vertical distribution of *Mastigoteuthis inermis*. Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *M. familica* except that the central organ is flatter and broadly continuous with the posterior organ. The posterior organ extends slightly beyond the insertion of the head retractor muscles and is less elongate.

Family Joubiniteuthidae

Joubiniteuthis portieri (Joubin 1912)

Vertical Distribution

Three specimens, all taken at night, were captured. One (42 mm ML excluding tail) was taken in an oblique tow between the surface and 425 m. A second specimen (64 mm ML) was taken in an opening-closing tow that fished between 480 and 550 m, and a third (85 mm ML) was taken in an open tow that fished at 1,125 m. Roper and Young (1975) listed the two known day captures of this species from the Atlantic Ocean as 800 to 900 m and 2,500 m.

Photosensitive Vesicles (Figure 27B)

One set of small organs is present. Each organ consists of a small number of globular vesicles that form a compact organ. Each organ is attached to the posteroventral margin of the optic stalk.

Family Cranchiidae

Liocranchia valdiviae (Chun 1906)

Vertical Distribution (Figure 29)

Both larvae and adults captured by the Tucker trawl are plotted. IKMT captures have been added where data are weak: specimens >24 mm ML and all specimens captured above 600 m during the day. One hundred fourteen specimens are plotted. Although only a few shallow day captures were made, the vertical distribution pattern is clear: animals between 5 and 15 mm ML predominate in

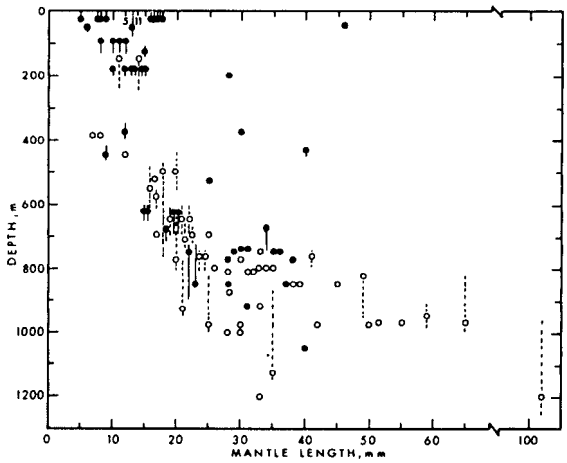

FIGURE 29.—Vertical distribution of *Liocranchia valdiviae*. Symbols as in Figure 1.

the upper few hundred meters. Descent to adult depths begins within the 5- to 15-mm ML size range or occasionally larger. Most specimens 15 to 25 mm ML are captured between depths of 500 and 700 m, while most animals ≥25 mm ML are found deeper than 700 m with progressively larger specimens found at progressively greater depths. Diel vertical migration does not occur. Five large specimens captured at depths of 40 to 525 m at night, however, indicate that some specimens occasionally wander into the upper depths at night. Mature specimens were not captured.

Photosensitive Vesicles (Figure 30A)

Liocranchia valdiviae has a single set of small organs. Each organ is elongate and extends along the posterior side of the optic stalk. Each organ usually consists of three elongated vesicles. A strip of dark brown screening pigment with irregular margins extends along much of the anteromedial edge of the ventral half of the organ. The broad dorsal vesicle either lacks screening pigment or has only a trace of it. The slender middle vesicle has a narrow, often discontinuous strip of pigment which widens ventrally. The ventral vesicle, which is the largest, has a broad, continuous layer of screening pigment.

The vesicles of *L. valdiviae* grow allometrically. At 30 mm ML the vesicles are small, and screening pigment consists of a single small patch on the ventral vesicle. In the largest specimen (102 mm ML), the pigment screen is very extensive and covers much of the anterior surface of the dorsal as well as ventral portions of each organ. The dorsal and ventral vesicles in each organ are somewhat broader in this specimen, making the organ more dumbbell shaped.

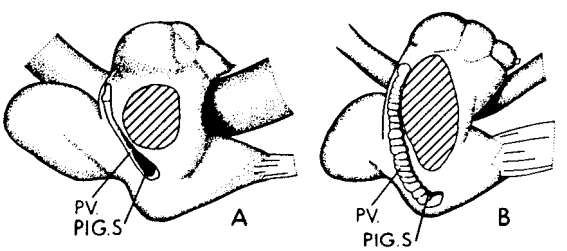

FIGURE 30.—A. Photosensitive vesicles of *Liocranchia valdiviae*. B. Photosensitive vesicles of *L. reinhardti*. Abbreviations as in Figure 2.

Liocranchia reinhardti (Steenstrup 1856)

Vertical Distribution (Figure 31)

All 12 juvenile specimens were captured at night. Ten of the 12 specimens were taken in the upper 100 m; the other 2 came from 150 to 200 m. A single mature specimen was captured at 775 m in a Tucker trawl that failed to close on retrieval. This specimen was a female that had recently spawned: remnants of what appeared to be sperm reservoirs were attached to the inner right wall of the mantle near the base of the funnel; the nidamental glands were gelatinous and extremely swollen; the ovary was depleted; and the muscular tissue of the mantle, fins, head, and arms was flaccid.

Unfortunately, there are no data on the day distribution of this species in Hawaiian waters.

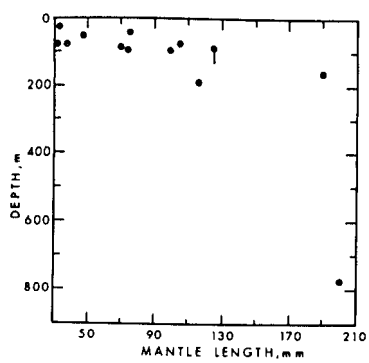

FIGURE 31.—Vertical distribution of *Liocranchia reinhardti*. Symbols as in Figure 1.

However, in the tropical North Atlantic, two specimens of *L. reinhardti* (44 and 48 mm ML) were captured during the day in opening-closing tows between 510 and 600 m, while a 75-mm ML specimen was taken in an open tow that fished between 390 and 800 m (C.C. Lu pers. commun.). Also, M. Clarke (1969) reported specimens of 46 and 69 mm ML from depths between 450 and 810 m during the day in the Atlantic.

Photosensitive Vesicles (Figure 30B)

The organs of *L. reinhardti* have been described by Messenger (1967a). This species has a single large set of organs lying along the posteromedial surface of the peduncle lobe. Each organ consists of a linear array of 20 to 25 tightly packed vesicles. The vesicles are elongated in a transverse direction except for those at the dorsal and ventral ends which are nearly circular. The vesicles are separated from one another by a heavy brown pigment screen which also covers most of the convex anterior side of the organ. Most vesicles within each organ thus form elongate cups which presumably admit light only from one surface. The dorsal vesicle, however, lacks screening pigment from the posterior lateral and dorsolateral surfaces. The ventral vesicle is larger, with photosensitive processes twice as long as those of the dorsal vesicle. It lacks pigment on its ventral and anterior surface. The curvature of the organ and the arrangement of screening pigment allows light to enter different vesicles from a wide range of angles.

Specimens ≤47 mm ML have no screening pigment on the vesicles while those ≥70 mm ML exhibit pigment as described above. The vesicles in the largest specimen (spent female) are slightly larger (especially the ventral vesicle) relative to the brain size than in smaller specimens.

Leachia pacifica (Issel 1908)

Vertical Distribution (Figure 32)

The vertical distribution of *L. pacifica* has been described elsewhere (Young 1975a). This species reaches about 80% of its maximum length in near-surface waters. Large specimens (45-60 mm ML) are found throughout the water column between 30 and at least 1,800 m with those taken from progressively deeper water exhibiting progressively greater sexual maturity. Gravid females were taken at depths >1,300 m.

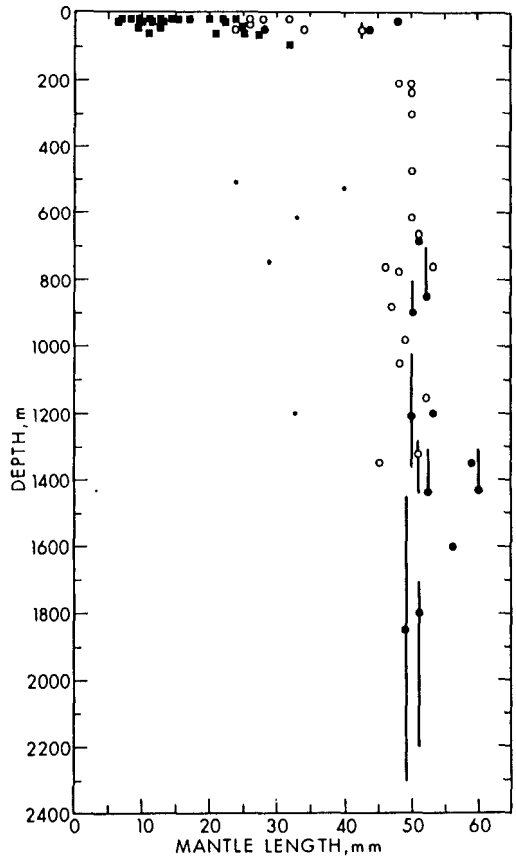

FIGURE 32.—Vertical distribution of *Leachia pacifica*. From Young (1975a). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 33A)

Leachia pacifica has a single set of organs located on the posteroventral surface of the peduncle lobe. Each organ consists of 4 or 5 cup-shaped vesicles that are closely packed into a small oval organ. A dark brown screening pigment covers

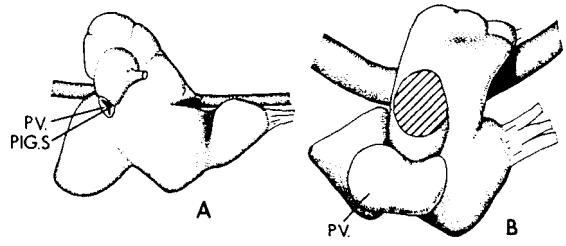

FIGURE 33.—A. Photosensitive vesicles of *Leachia pacifica*. B. Photosensitive vesicles of *Sandalops melancholicus*. Abbreviations as in Figure 2.

much of the anterior and slightly dorsal surface of each organ. This pigment is also found in the walls between some vesicles, tending to isolate them from one another. Although the vesicles are minute in the larva and very small in the adults, a small positive allometric growth of the vesicles seems to occur. Screening pigment first appears on the vesicles between about 20 and 30 mm ML. In the adult, the screening pigment is most extensive and covers the entire anteromedial surface of the organ.

Phasmatopsis fisheri (Berry 1909)

Vertical Distribution (Figure 34)

Over 300 specimens of *P. fisheri* were captured but most were larvae. Metamorphosis occurs at a size of 40 to 50 mm ML.

During the day, six larvae were captured between 150 and 250 m. Seventeen juvenile and adult specimens were captured between about 625 and 800 m; most captures were made between 650 and 775 m.

At night, larvae ≤30 mm ML were taken primarily in the upper 50 m; larvae 31 to 40 mm ML were found throughout the upper 200 m. Fourteen juveniles and adults were taken at night between 90 and 225 m; most captures were made between 100 and 200 m.

Photosensitive Vesicles (Figure 35)

Phasmatopsis fisheri has a single set of large organs. Each organ consists of a broad, elongate vesicle that extends from the optic gland on the dorsal surface of the optic stalk ventrally over the posterior surface of the peduncle complex onto the side of the ventral subesophageal mass, where it

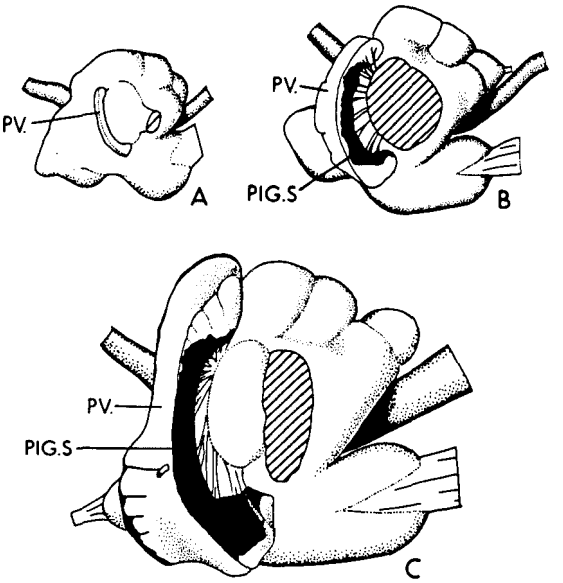

FIGURE 35.—Photosensitive vesicles of *Phasmatopsis fisheri*. A. Larva, 35 mm ML. B. Juvenile, 70 mm ML. C. Adult, 130 mm ML. Abbreviations as in Figure 2.

bends slightly dorsally. Each organ is thick laterally and medially. Most of the anterior, medial, and lateral surfaces of each organ are covered by dark brown pigment screen. The dorsal tip of each organ lacks screening pigment on its lateral portion and has limited pigment screen on its medial portion. The curvature of each organ allows light to enter various parts from a wide range of angles.

The anterior wall of each organ consists of little more than a membrane backed by dense pigment. The posterior wall and the walls of the dorsal and ventral ends of each organ contain 4 or 5 layers of sensory-cell bodies. Sensory processes are longer (215 μm) and thinner (inner diameter 2 to 4 μm) in the ventral parts of the organ than in the dorsal

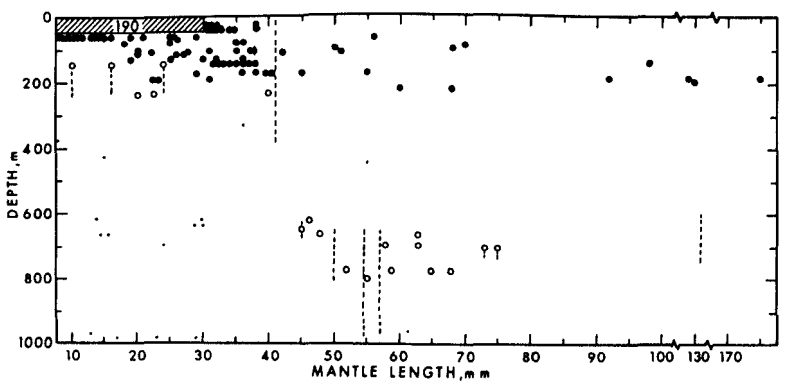

FIGURE 34.—Vertical distribution of *Phasmatopsis fisheri*. Symbols as in Figure 1.

parts (length 155 μm, inner diameter 3 to 6 μm). The processes are long and slender and organized in a straight, parallel alignment.

Each organ is small in larvae and lacks screening pigment. At 35 mm ML, the vesicles form a narrow strip along the posterior surface of the peduncle lobe (Figure 35A). The largest larvae have relatively small organs without screening pigment; the youngest juveniles have large organs that are heavily pigmented. In the juvenile and adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the brain. The ventral half of the organ is particularly enlarged and the organs on each side of the brain contact broadly (but do not fuse) below the ventral midline of the brain.

Taonius pavo (LeSueur 1821)

Vertical Distribution (Figure 36)

The vertical distribution of *T. pavo* has been described by Young (1975d). Larvae probably live in the upper 400 m, although only one capture was made. Juveniles were found primarily between 600 and 650 m, and adults were captured between 725 and 970 m. Diel vertical migration does not occur.

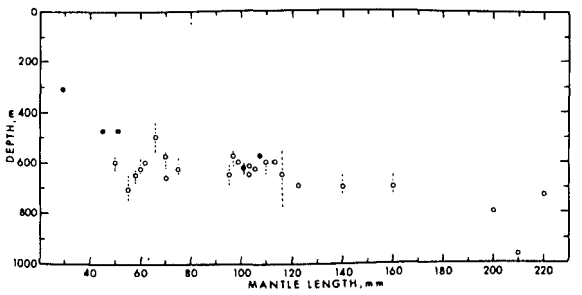

FIGURE 36.—Vertical distribution of *Taonius pavo*. From Young (1975d). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 37)

Taonius pavo has a single set of organs located on the posteroventral side of the peduncle complex. Each organ consists of a single oval vesicle. No screening pigment is present. The large size of the vesicle in a 220-mm ML specimen belies its internal structure. The large central region of the

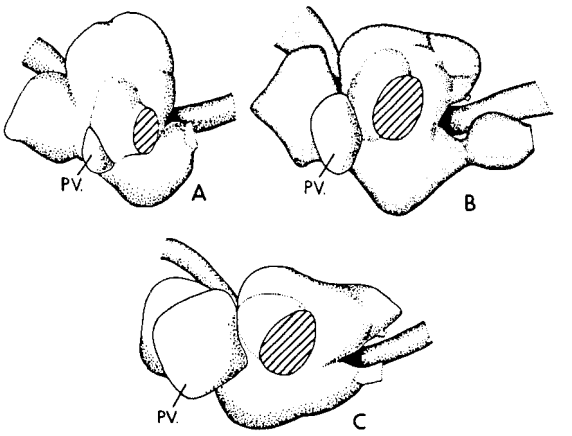

FIGURE 37.—Photosensitive vesicles of *Taonius pavo*. A. Larva. B. Juvenile, 140 mm ML. C. Adult, 220 mm ML.

lumen is unoccupied. Sensory processes occupy about 1/5 (i.e., about 230 μm) of the lumen diameter on the anterior, posterior, and dorsal sides and slightly more (about 300μm) on the ventral sides. The processes are loosely packed and intertwined to a large extent dorsally and more tightly packed ventrally. Inner diameters of the processes vary greatly from about 3 to 30 μm. The wall on the dorsal half of the organ contains about two layers of sensory-cell bodies compared with about three layers ventrally. In a 140-mm ML juvenile, the dissected vesicle was also hollow, with an even thinner region of the lumen occupied by sensory processes. The organs exhibit positive allometric growth (Figure 37).

Sandalops melancholicus Chun 1906

Vertical Distribution (Figure 38)

The vertical distribution in this species has been reported by Young (1975d). Larvae were found in the upper 400 m. Juveniles were captured between 450 and 674 m, and two adults were captured near 800 and 1,075 m. Diel vertical migration does not occur.

Photosensitive Vesicles (Figure 33B)

Sandalops melancholicus has a set of organs located along the ventral surface of the peduncle complex. Each organ consists of a single bilobed vesicle (R. E. Young 1977). Slight positive allometric growth of the vesicles occurs between the juvenile and adult stages.

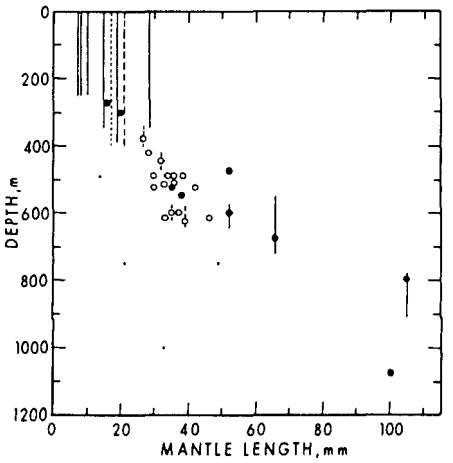

FIGURE 38.—Vertical distribution of *Sandalops melancholicus*. From Young (1975d). Symbols as in Figure 1.

Helicocranchia beebei Robson 1948

Vertical Distribution (Figure 39)

Including larvae, 47 specimens were captured. Although day and night captures are not well intermingled in Figure 39 (due largely to sampling inequities), the data indicate that this species does not migrate. Rather, it seems to undergo ontogenetic descent. The youngest specimens were captured between 100 and 200 m. Progressively larger specimens were generally taken at progressively greater depths, although the relationship of size to depth is not very precise. The deepest capture was probably at 1,200 m. Mature specimens were not captured.

Photosensitive Vesicles (Figure 40A)

One set of organs is present. Each organ consists of a single small oval vesicle located on the posterior surface of the peduncle complex. No screening pigment is present. Very slight, if any, positive allometric increase in the size of the vesicles occurs from juveniles to the largest specimens.

Bathothauma lyromma Chun 1906

Vertical Distribution (Figure 41)

Although only 12 specimens were captured, a general pattern of ontogenetic descent is evident.

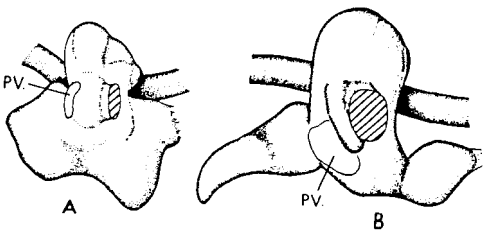

FIGURE 40.—A. Photosensitive vesicles of *Helicocranchia beebei*. B. Photosensitive vesicles of *Bathothauma lyromma*. Abbreviations as in Figure 2.

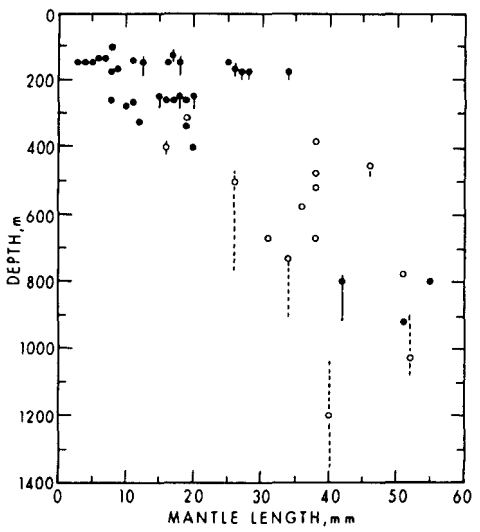

FIGURE 39.—Vertical distribution of *Helicocranchia beebei*. Symbols as in Figure 1.

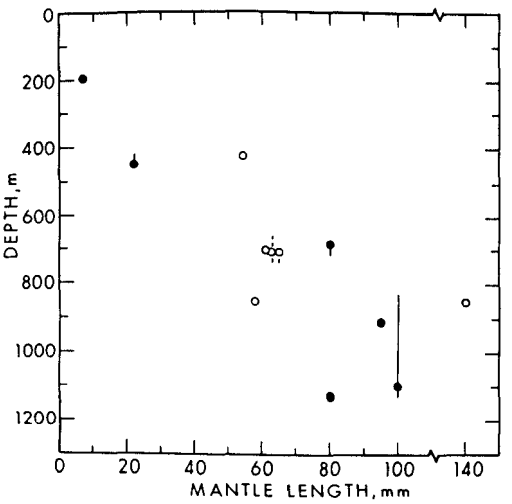

FIGURE 41.—Vertical distribution of *Bathothauma lyromma*. Symbols as in Figure 1.

Day and night captures were in the same depth range, indicating that diel vertical migration does not occur. The three specimens captured at the greatest depths were gravid females. The specimen captured at 910 m had sperm receptacles imbedded in the back of the head and in the anterodorsal surface of the mantle. The nidamental and oviducal glands were greatly enlarged and the entire visceropericardial coelom was packed with large eggs. The muscular tissue was slightly flabby. The specimen captured at 1,125 m exhibited almost identical features. The specimen captured at about 1,100 m had similarly placed sperm reservoirs, less extensively enlarged nidamental and oviducal glands, and lacked eggs (apparently due to damage during capture). This specimen exhibited no sign of muscular degeneration. The mantle cavity of this specimen had two very long arms from another specimen (presumably a male) attached to the inner wall of the mantle. The largest specimen was an immature female. Its size was largely due to its fixation in a relaxed state. In this species, the pen is extraorinarily delicate and accurate measurements of contracted, crumpled specimens are nearly impossible.

Photosensitive Vesicles (Figure 40B)

Bathothauma lyromma has a single set of organs. Each organ consists of a flat oval vesicle located on the posteroventral surface of the peduncle complex. No screening pigment is present. Slight positive allometric growth of the vesicles occurs from juveniles to adults.

Galiteuthis pacifica (Robson 1948)

Vertical Distribution (Figure 42)

The 27 specimens captured indicate a broad vertical range for this species. Fourteen of the 19 captures of specimens >20 mm ML came from depths of 700 m or more. The data indicate that diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles of this species are similar to those of *G. phyllura* described by Young (1972a). A single set of organs is present. Each organ consists of a large oval vesicle attached to the posteroventral surface of the peduncle complex. Considerable positive allometric growth of the vesicles occurs.

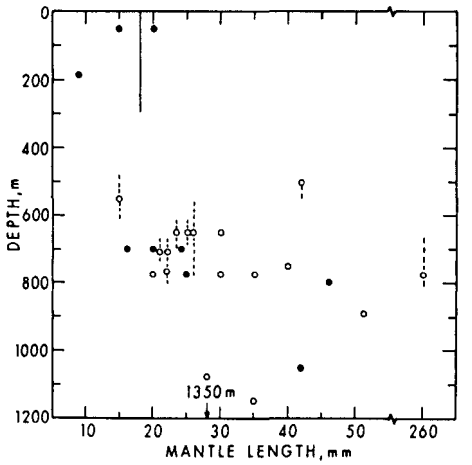

FIGURE 42.—Vertical distribution of *Galiteuthis pacifica*. Symbols as in Figure 1.

Order Octopoda

Family Bolitaenidae

Eledonella pygmaea Verrill 1884

Vertical Distribution (Figure 43)

Eighty specimens were captured. Day and night captures were in the same depth range (except above 300 m where day trawling was minimal), indicating that diel vertical migration does not occur. Most specimens between 5 and 15 mm ML

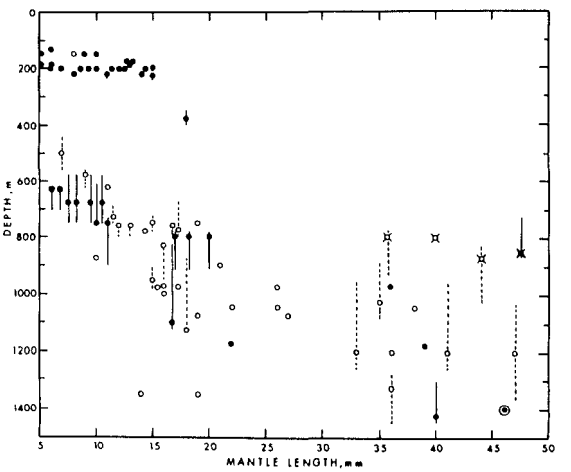

FIGURE 43.—Vertical distribution of *Eledonella pygmaea*. Circles with crosses represent brooding females. Double circle represents a gravid female. Otherwise symbols as in Figure 1.

were captured either around 200 m or below 600 m. Apparently the size at which young begin their descent to adult depths is rather variable. The deep captures exhibit a clear pattern of ontogenetic descent. At 25 mm ML or larger all specimens (excluding brooding females) were captured between depths of 975 and 1,425 m. Four females, apparently brooding, were captured between about 800 and 870 m.

The pigmentation of the female changes as she becomes gravid: the chromatophores over the mantle and especially over the aboral surface of the arms and web become more numerous, and the oral surfaces of the arms and web develop an even denser pigmentation. Nearly all iridophores are lost. At the same time the arms and the web become thicker. The web between the dorsal six arms becomes more extensive, and the web between the two ventral arms is reduced. These dark octopods spawn and apparently brood their young (Young 1972b). Five specimens taken from horizontal tows exhibited this increased pigmentation. In four cases, the ovary was depleted, and in the fifth, captured at 1,400 m, the eggs were not fully mature, but were considerably larger than in an immature female of approximately the same size. In two cases egg strings with developing embryos were found in the same trawl with dark and presumably brooding females.

No mature males were taken. However, judging from the development of the hectocotylus, the penis, and the spermatophore glands, two specimens captured at 1,200 and 1,425 m were nearly mature. Another slightly less mature specimen was taken at 1,325 m. Three still less mature specimens were taken between 1,175 and 1,200 m, while a large male taken at 1,025 m was the least developed of all.

Photosensitive Vesicles (Figure 44A)

The photosensitive vesicles consist of a single pair of organs; each organ is a spherical vesicle attached to the posterior margin of the stellate ganglion.

Japetella diaphana Hoyle 1885

Vertical Distribution (Figure 45)

Seventy-four specimens were captured. Diel vertical migration does not occur. Specimens <20 mm ML were captured mostly in two regions, between 170 and 270 m and between 500 and 800 m,

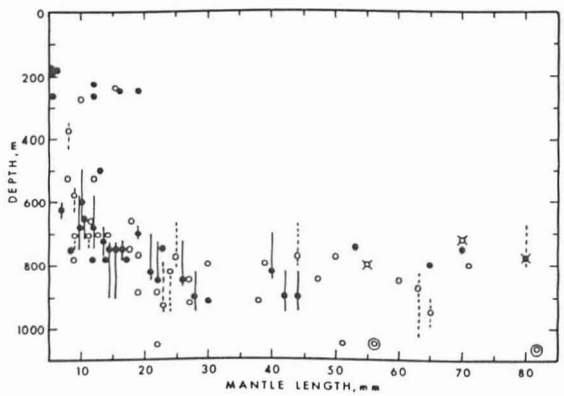

FIGURE 45.—Vertical distribution of *Japetella diaphana*. Circles with crosses represent brooding females. Double circles represent gravid females. Otherwise symbols as in Figure 1.

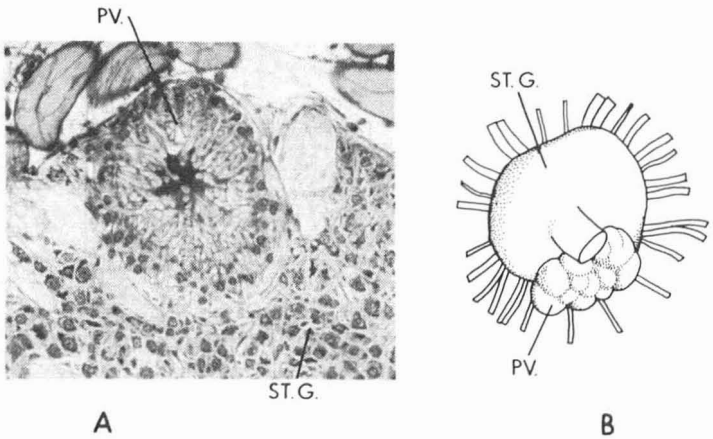

FIGURE 44.—A. Section through the photosensitive vesicle of adult *Eledonella pygmaea*. B. Photosensitive vesicles of *Amphitretus pelagicus*. ST. G.—Stellate ganglion. Otherwise symbols as in Figure 1.

where they exhibited an ontogenetic descent. The depth range for specimens ≥20 mm ML was 725 to 1,065 m; nearly 90% of the animals occur between 700 and 950 m and nearly 60% between 750 and 850 m. Gravid and brooding females were found at the extremes of this range. Two gravid females were captured at 1,050 and 1,065 m while three spent and presumably brooding females were taken between 725 and 800 m. As in *E. pygmaea,* the gravid and spent females have a very heavy pigmentation and lack most of the iridophores present in younger specimens. Five such females were captured in horizontal tows. One gravid female with a sperm mass embedded in the gelatinous tissue between the second and third arms was taken at 1,050 m. Another taken at 1,065 m had been gutted in the trawl but had not spawned: the musculature was firmer than in spent females, and the catch contained a large number of octopod eggs which undoubtedly came from the ruptured ovary. Three specimens taken between 725 and 800 m probably had spawned: two had depleted ovaries and the third was gutted but had deteriorated musculature. In the same tow with the last specimen were four newly hatched larvae, presumably from the brood of the female. One large, heavily pigmented female taken in an oblique tow had the remnants of an egg string dangling from one of the large suckers of the third arm. Two eggs were completely engulfed by the sucker, while a third dangled from the broken egg string extending from the sucker. No mature males were taken.

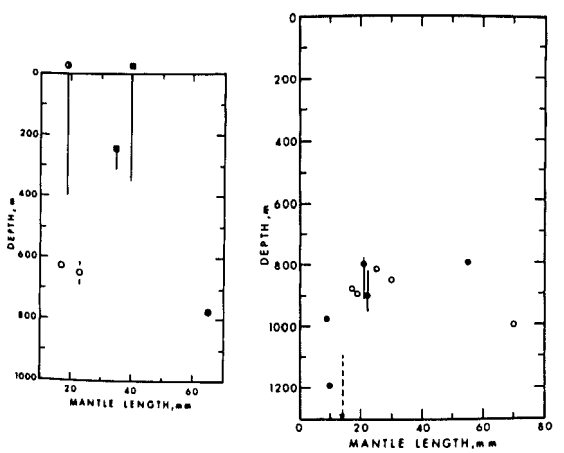

FIGURE 46.—A. Vertical distribution of *Amphitretus pelagicus* (squares) and *Vitreledonella richardi* (circles). B. Vertical distribution of *Vampyroteuthis infernalis*. Half-closed circles represent a twilight capture. Otherwise symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *E. pygmaea.*

Family Amphitretidae

Amphitretus pelagicus Hoyle 1885

Vertical Distribution (Figure 46A)

Two specimens were taken at night in the upper 350 m.

Photosensitive Vesicles (Figure 44B)

Amphitretus pelagicus has one set of organs. They lie on the stellate ganglia immediately anterior to the entry points of the pallial nerves. Each organ consists of a large complex of a dozen or more generally circular vesicles which cover most of the anterior wall of the ganglion.

Family Vitreledonnelidae

Vitreledonnella richardi Joudin 1918

Vertical Distribution (Figure 46A)

Four specimens were captured. One small specimen was taken in an oblique twilight tow between the surface and 400 m. Two other small specimens were taken between 600 and 650 m during the day. One large specimen was captured at 775 m during the night.

Photosensitive Vesicles

An organ consisting of a single spherical vesicle is located on the posterior margin of each stellate ganglion.

Order Vampyromorpha

Family Vampyroteuthidae

Vampyroteuthis infernalis Chun 1903

Vertical Distribution (Figure 46B).

Eleven specimens were captured. Ten of the 11 were taken between depths of 800 and 1,200 m. The remaining specimen came from an open oblique tow that fished between 1,100 and 1,900 m. Diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles have been described in detail by Young (1972a). One set is present. They are located in the dorsal wall of the mantle cavity at the base of the funnel. Each organ consists of a small cluster of spherical vesicles.

Order Sepioidea

Heteroteuthis hawaiiensis (Berry 1909)

Vertical Distribution (Figure 47)

The distribution of this species has been discussed by R. E. Young (1977). During the day, specimens ≤17 mm ML were taken between 250 and 350 m; larger specimens were taken between 375 and 650 m. At night, most specimens <17 mm ML came from depths between 150 and 200 m; larger specimens were taken between depths of 110 and 550 m. Males and females mature at about 15-16 mm ML.

Photosensitive Vesicles (Figure 48)

Two sets of organs are present (R. E. Young 1977). The more dorsal set lies on the posterior margin of the peduncle complex and consists of a short and narrow string of tiny vesicles. An even

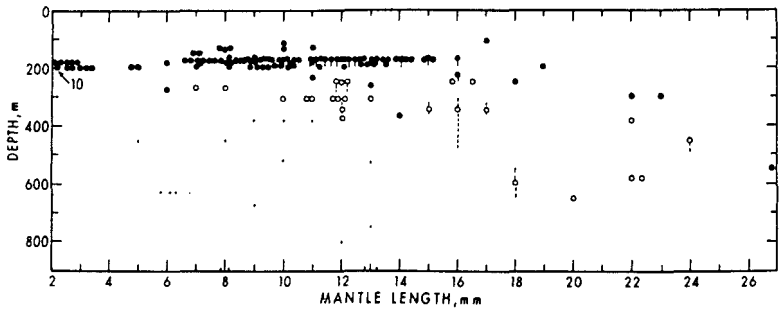

FIGURE 47.—Vertical distribution of *Heteroteuthis hawaiiensis*. From R. E. Young (1977). Symbols as in Figure 1.

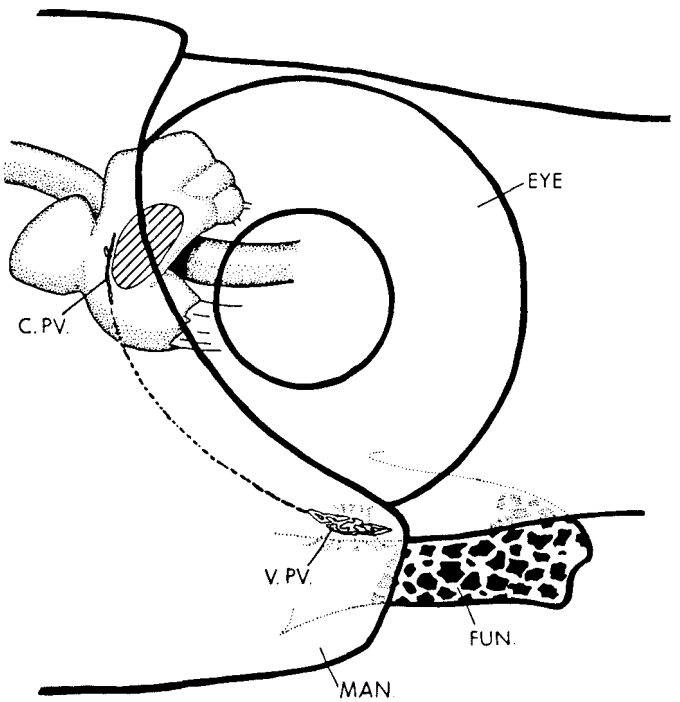

FIGURE 48.—Photosensitive vesicles of *Heteroteuthis hawaiiensis*. In this figure the outline of portions of the head and mantle are superimposed to give a clear perspective of the peculiar arrangement of vesicles in this species. EYE—eye; FUN.—funnel; MAN.—mantle. Otherwise abbreviations as in Figure 2.

narrower string of tiny vesicles extends ventrally around the eyes and joins a rather large but extremely thin, loosely associated group of vesicles that lies over the lateral base of the funnel.

DISCUSSION

Vertical Distribution

The numbers of cephalopod species taken in different 100-m depth zones for the upper 1,400 m showed a broad peak between 500 and 800 m during the day (Figure 49). An abrupt increase in the number of species near 400 m was obscured by the method of analysis: eight species occurred for the first time between depths of 375 and 450 m. To indicate faunal change, the number of species found for the first time in each zone (i.e., depth zones containing species upper range limits) were compared with zones where species found in lesser depths were absent for the first time (i.e., depth zones immediately below the lower range limits) (Figure 49).

The peak at 700-800 m in the summed plot of species added and species lost indicates that many species dropped out in the 600-700 m zone and many were added in the 700-800 m zone. The chart also indicates that only two species were encountered for the first time at 800 m or below. One was the poorly sampled *Brachioteuthis* sp. and the other was deep-living *Vampyroteuthis infernalis*. The data indicate peak species richness in the upper few hundred meters with relatively little change between 300 and 1,000 m during the night (Figure 49).

Numbers of individuals in different depth zones in the upper 1,400 m (exclusive of young individuals, captures in oblique tows, and contaminants) were also examined (Figure 50). During the day, the greatest abundance of individuals occurred between 400 and 700 m. This peak reflects the dominance of the enoploteuthids, especially *Pyroteuthis* and *Pterygioteuthis* spp. The high rate of capture in the 300- to 400-m zone was due in part to a few species whose upper limits extended slightly above 400 m. Nevertheless, an abrupt increase in number occurred in the 400- to 500-m zone. The rates of capture below 1,000 m were unreliable due to the small amount of trawling.

The night data in the upper 400 m were lumped into 50-m increments due to greater control over trawling depths in near-surface waters. The largest catches at night were made in the upper 200 m. In this region two peaks were apparent (Figure 50). The peak in the 50- to 100-m zone was largely due to *Pterygioteuthis microlampas*, the

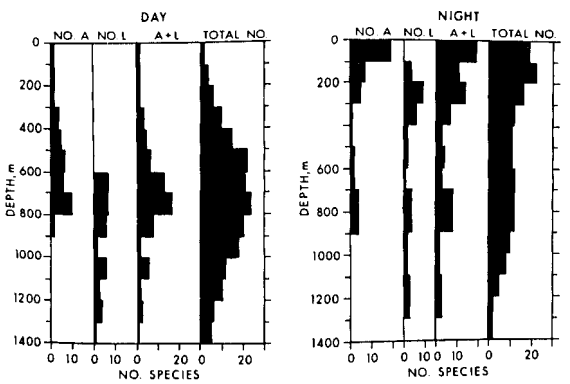

FIGURE 49.—Numbers of species versus depth. The histograms were based on species ranges from midwater trawl data. Data were lumped into 100-m depth increments and were not corrected for unequal trawling times at different depths. Data for some species were very meager. Young stages found in near-surface waters that can be distinguished by an abrupt change in habitat or by a metamorphosis have been eliminated from the figures. No. A—number of species added (i.e., found for the first time in a given depth zone). No. L.—number of species lost (i.e., absent from a given depth zone but present in the shallower zone). A + L—sum of two previous histograms. Total No.—total number of species in each depth zone.

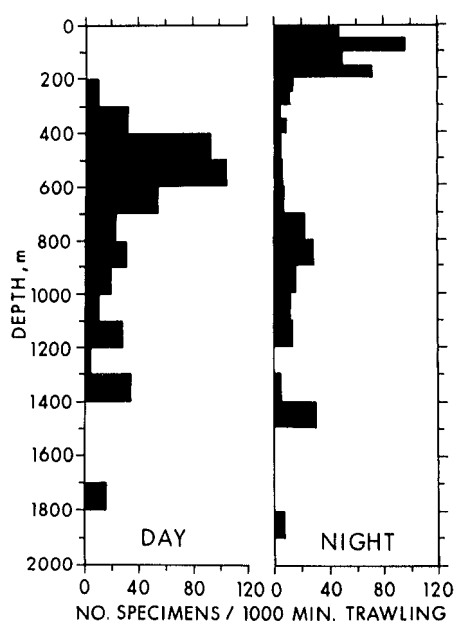

FIGURE 50.—Total catch rate of numbers of cephalopod specimens from both trawls.

most abundant species in the collection. The peak in the 150- to 200-m zone was largely due to *Pyroteuthis addolux* and *Heteroteuthis hawaiiensis*; young *Histioteuthis dofleini* also contributed considerably. Young *Eledonella* were also found in this zone although they were excluded from the figures as "larvae."

The zone between 200 and 700 m was sparsely inhabited at night. The peak between 700 and 1,000 m represented the deep nonmigrating population. The capture rate in this region was almost identical to the day capture rate at the same depths: deep-living migrators were few.

The total rate of capture for the water column during the day was 459 specimens/1,000 min of trawling. Surprisingly, the total capture rate at night was only 309 specimens/1,000 min. This difference was largely due to smaller-than-expected catches at night in the upper 200 m of the few most abundant species. The reason for the low night catches is unknown. Another estimate of the number of animals in the upper 250 m at night was obtained by assuming that the day peak from 300 to 700 m (minus the night catch at these depths) shifted into this upper zone at night (see below). On this basis, nearly 80% of the individuals occurred in the upper 250 m at night. If one considers also the abundant ommastrephids which avoided midwater trawls but occurred in near-surface waters at night, then only a small percent of the total number of individuals would remain below 250 m at night.

In many species, most of the population shifted upward at night. Such day-night differences existed in at least 25 of the 47 species examined, based on present data and literature records. Adequate data were lacking for ommastrephids and *Neoteuthis* sp. Therefore, where the vertical ranges are known, nearly 60% of the species exhibited diel shifts in habitat. Species not exhibiting diel migrations belonged primarily to the Cranchiidae (seven species) and the Octopoda (five species).

At least 18 of the 25 species that exhibited diel migrations occurred almost exclusively in the upper 250 m at night. These included all 11 enoploteuthids, *Liocranchia reinhardti*, *Phasmatopsis fisheri*, *Ctenopteryx siculus*, *Octopoteuthis neilseni*, *Brachioteuthis* sp., *Chiroteuthis* sp., *Onychoteuthis compacta*, and young *Heteroteuthis hawaiiensis*. Two species for which the data were incomplete (*Cycloteuthis serventyi* and *Chiroteuthis picteti*) probably belonged to this category as well. Therefore, at least 80% of the migratory species occurred in the upper 250 m at night.

Amesbury (1975) examined vertical zonation of midwater fishes during the day off Hawaii. He concluded that the water column could be divided into three regions: epipelagic, mesopelagic, and bathypelagic zones. The boundary between the epipelagic and mesopelagic zones occurred at about 400 m and was marked by a sharp increase in the numbers of individuals. This boundary appeared to apply equally well to cephalopods. The boundary between the mesopelagic and bathypelagic zones occurred at about 1,200 m. This boundary was marked by a noticeable decrease in fish numbers and represented the greatest day depths of vertically migrating fish. This lower boundary was not applicable to cephalopods; there was no comparable decrease in numbers of individuals; and this depth seemed to be well below the range of vertical migrators. Amesbury further divided the mesopelagic zone into upper and lower zones with the boundary at about 650 to 700 m. Cephalopods exhibited maximum species turnover at about this depth, as well as changes in light-related adaptations in some species (Young 1975d). Although fish and cephalopod distributions differed with respect to the lower boundary, the distribution of cephalopods generally supported Amesbury's zonation.

In spite of the rather small size of the collection, some evidence of vertical habitat separation among closely related species emerged. Three of the more abundant species belong to the subfamily Pyroteuthinae: *Pyroteuthis addolux*, *Pterygioteuthis microlampas*, and *P. giardi*. In general body proportions and armature, *P. microlampas* was more similar to *Pyroteuthis addolux* than to its congener. During the day, these two species occupied the same depths around 500 m. At night, their populations peaked at distinctly different depths: *Pterygioteuthis microlampas* occurred primarily between 50 and 100 m, while *Pyroteuthis addolux* occurred primarily between 150 and 200 m. Although the data were less clear for *Pterygioteuthis giardi*, this species seemed to center around 400 m during the day and in the upper 100 m at night with about half of the population in the upper 50 m. Thus this species was shallower than its two relatives during the day and tended to be shallower at night, although broad overlap occurred with its congener.

Two species of the genus *Abralia* occurred off Hawaii. *Abralia trigonura* was a common vertical migrator in the area sampled of the open ocean, while *A. astrosticta* was never taken there. *Abralia astrosticta* seems to be a vertical migrator that moves in close proximity to the ocean floor (Roper and Young 1975).

Two species of *Mastigoteuthis* were taken. Both species shared the same day habitat at 700 to 800 m. At night, the population of *M. inermis* spread upward in the water column 400 or 500 m. Although the data were few, *M. famelica* appeared to spread little or not at all.

One of the clearest cases of habitat separation of congeners occurred in *Liocranchia*. *Liocranchia valdiviae* was taken in lower mesopelagic depths during the day and it did not migrate. *Liocranchia reinhardti* was taken in near-surface waters at night and apparently occurred in upper mesopelagic depths during the day.

Although the octopods *Japetella diaphana* and *Eledonella pygmaea* are placed in separate genera, they are very closely related. Both were taken in deep waters and did not migrate. The adults (except brooding females) were taken at distinctly different depths: *E. pygmaea* occupied depths from 975 to 1,425 m while *J. diaphana* occupied depths primarily from 700 to 950 m. Young stages prior to descent were found in near-surface waters. In this habitat *E. pygmaea* was captured primarily at 200 m or just above while *J. diaphana* was captured primarily below 200 m. Young stages of both species in the process of descent occupied depths of about 400 to 800 m or more. The data indicated, however, that at any given size, except for those just beginning descent, the young of *E. pygmaea* occupied greater depths than the young of *J. diaphana*.

In the genus *Abraliopsis* three species were taken: *Abraliopsis* sp. A and *Abraliopsis* sp. C form the most closely related species pair. The available data show no obvious habitat differences. Although the more common *Abraliopsis* sp. A reached a considerably larger size than species C (43 mm ML vs. 33 mm ML), young individuals of species A, however, apparently cooccurred with species C of the same size. The day and night habitats of *Abraliopsis* sp. B were not separable from its two congeners.

Three other groups of congeners were taken (i.e., in *Enoploteuthis*, *Histioteuthis*, and *Chiroteuthis*). No differences in habitats were found within these groups; however, the data were extremely sparse.

Reproduction

Young (1972b) presented evidence for brooding in *Eledonella pygmaea* (incorrectly reported as *Bolitaena microcolyla*) and suggested that brooding occurs in all pelagic octopods. Additional evidence from the present study substantiated the brooding habit for *E. pygmaea*. In addition, evidence indicating brooding in the octopod *Japetella diaphana* was found. This species underwent changes at maturity similar to *E. pygmaea*. Further, newly hatched young have been found in the same trawl with spent females, and in one case the remnants of an egg string was found attached to an arm sucker of such a female.

In both species, gravid or near-gravid females were taken only at the lower limits of the species' vertical range. Although mature males were not taken, those nearest maturity were also taken in the lower parts of the depth range. Apparently, mating takes place at the lower depth limits of the population. Brooding females, on the other hand, were found only at the upper limit of the adult population in *J. diaphana* and only well above the upper limit of the remaining adult population in *E. pygmaea*. The brooding females of both species occurred around 800 m. Presumably the females migrate upward to around 800 m either just before or just after spawning. The increased risk of predation above 800 m probably prevents the female from further upward movement: the numbers of fishes increase greatly above 800 m (Amesbury 1975), and visual detection of the large silhouette presented by a brooding female should be possible above about 750 to 775 m (Young and Roper 1977). The upward movement must be unrelated to feeding since brooding females do not feed (Young 1972b). The upward migration may simply decrease the distance the young must travel after hatching to their larval habitat near 200 m.

A number of cephalopods may spawn at the lower end of their depth range. Evidence for deep-spawning was found in several vertically migrating species. A single spent female of *Liocranchia reinhardti* was captured at 775 m at night, well below its normal night habitat in the upper 200 m. A single gravid, mated female of *Brachioteuthis* sp. was captured at 1,125 m at night; its normal night habitat is in the upper 200 m. *Heteroteuthis hawaiiensis* migrated vertically and exhibited

narrow vertical ranges day and night until sexual maturity was reached; a poorly defined ontogenetic descent then ensued. Unfortunately, no other clues to spawning depth are known.

The nonmigrating species that exhibit a gradual ontogenetic descent would be expected to spawn at the lower end of their range. Indeed, this appeared to happen in *Bathothauma lyromma*. The most dramatic example occurred in *Leachia pacifica*. Young (1975a) demonstrated that this species descends near the time of sexual maturity from near-surface waters to depths of 1,000 to 2,000 m to mate and spawn.

Larvae of most pelagic oceanic cephalopods occur in near-surface waters. Upward migration of larvae would seem to be a formidable task for species that spawn at great depths. The deep-living octopods apparently carry their young partway up presumably to lighten this task. Perhaps squid egg masses are positively buoyant and float to the surface. There are a number of observations of egg masses of pelagic cephalopods floating at or near the ocean surface (see Clarke 1966). However, these have yet to be shown to belong to a deep-spawning species.

Photosensitive Vesicles

These vesicular organs were present in all Hawaiian pelagic cephalopods and they occurred in a great variety of shapes, sizes, and locations. In many squids, the organs were subdivided into as many as four sets of separate organs. In squid, the organs were always found within the confines of the cephalic cartilage and were located either on the optic stalk (central organs) or dorsal, posterior, or ventral to the optic stalk (dorsal, posterior, and ventral organs, respectively). The separate organs often faced different directions (i.e., their broadest surface faced a dorsal, posterior, or ventral direction).

These separate organs were frequently associated with distinctive "windows" in the overlying skin bearing few if any chromatophores. Such windows seem to be unnecessary since most cephalopods can become quite transparent by contraction of their chromatophores. The windows in combination with the more pigmented surrounding skin, however, may restrict light to specific receptors and thereby improve the directionality of the organs. In a few cases (e.g., *Phasmatopsis fisheri* and *Ctenopteryx siculus*), the organ was not subdivided but elongate and curved, allowing different portions of a single organ to face various directions. A directional response of each portion was insured either by heavy pigment (e.g., *P. fisheri*) or silvery iridophores (*C. siculus*) which shielded one surface of the organ. Not all species, however, had vesicular organs that could discriminate between dorsal, posterior, and ventral sources of light. Some species had undivided central organs (e.g., *Sandalops melancholicus, Taonius pavo*) without apparent screening devices which therefore are nondirectional. In others, the total area surveyed by a nondirectional organ was restricted by its cryptic position (e.g., *Vampyroteuthis*). Clearly not all cephalopods use these organs in the same way.

General trends between organ size and habitat depth during the day occurred in these animals. Teuthoids and sepioids found in the upper 400 m (neritic species and young *Heteroteuthis hawaiiensis*) generally had small organs. Species found primarily between 400 and 700 m generally had large, complex organs. These included most enoploteuthids, histioteuthids, probably *Discoteuthis laciniosa*, *Liocranchia reinhardti*, and young *Taonius pavo*. Between 700 and 800 m, species with large, complex organs (i.e., *Ctenopteryx siculus, Phasmatopsis fisheri, Thelidioteuthis allessendrinii, Cycloteuthis serventyi*, probably large *Octopoteuthis nielseni*, adult *Taonius pavo*, and *Galiteuthis pacificus*, and *Bathyteuthis abyssicola*) cooccurred with species which had small organs (i.e., chiroteuthids, *Mastigoteuthis*, *Grimalditeuthis bomplandii*, large *Liocranchia valdiviae*, and probably *Neoteuthis* sp.). Many of the small-vesicle species had ranges that extended well below 800 m, where they were joined by other small-organ species (i.e., *Vampyroteuthis infernalis* and probably *Joubiniteuthis portieri*).

The relationship of organ size to habitat depth was especially marked in young *Phasmatopsis fisheri*. The epipelagic larvae of *P. fisheri*, which may grow to 40 and 50 mm ML had small central vesicles. Upon metamorphosis and descent to the adult day habitat (650-775 m), the organs became greatly enlarged (Figure 34). As growth continued, however, a gradual positive allometric growth of the organs occurred without a clear increase in habitat depth.

A number of species did not follow these general trends. Several cranchiids exhibited gradual ontogenetic descent; one of these (*Helicocranchia beebei*) had small organs, while the others (*San-*

dalops melancholicus and *Bathothauma lyromma*) had large organs. *Leachia pacifica*, which had small organs, spent most of its life in epipelagic waters and then descended to depths >1,000 m. *Onychoteuthis compacta* seemed to range widely during the day and had rather large organs (its habitat, however, is poorly known). *Brachioteuthis* had similar organs but probably occurred below 800 m during the day. The ommastrephids had a complex arrangement of organs, yet these animals were primarily epipelagic. In juveniles of many species (e.g., enoploteuthids), the size of the organs (relative to the size of the brain) may be large; yet their absolute size was small when compared with adults occupying the same depths.

Compared with squid, all octopods had small organs. With the probable exception of the tubular eyed *Amphitretus pelagicus*, octopods probably do not occupy depths between 400 and 700 m during the day except as juveniles in transit to greater depths. *Amphitretus pelagicus* is the only pelagic octopod that exhibited clear modification of its organs. In contrast to the small organs, each consisting of a single vesicle, of other octopods, this animal has a larger organ composed of many separate vesicles.

Presumably the general trends with depth were related to depth gradients in both downwelling daylight and bioluminescent light. Downwelling daylight decreases exponentially with depth. Bioluminescent activity should increase from 400 to 600-800 m then decline rapidly if numbers of midwater fishes at various depths (see Amesbury 1975) provide an index to bioluminescent activity during the day. While many vesicles may detect both downwelling skylight and bioluminescent light, we will examine evidence for these two functions separately.

The eyes of some mesopelagic animals can probably detect silhouettes at depths of 750 to 775 m (Young and Roper 1977). Presumably some photosensitive vesicles are at least as sensitive as the eyes, especially when we consider the large size and apparent high pigment density of some (see Young 1972a). The large dorsal organs of squid were positioned so they are exposed to downwelling daylight. Large central organs appeared to be exposed to this light in species lacking dorsal organs.

Some experimental evidence indicates that midwater cephalopods detect downwelling light with these vesicular organs. A number of cephalopods have been seen to conceal themselves with bioluminescent light (Young and Roper 1977). This counterillumination requires that the intensity of downwelling light is precisely determined by the animal, and the photosensitive vesicles seem the likely photoreceptor (Young 1973, 1977). Recently R. E. Young, C. F. E. Roper, and J. Walters (in manuscr.) covered the dorsal organs of *Abraliopsis* sp. B while it was counterilluminating and recorded a 90% drop in its luminescence. They concluded that the dorsal organs detect downwelling light. Since animals can detect downwelling light with these organs for counterillumination, they may use this photic information for other purposes as well.

Vertical migration in many midwater animals is closely associated with changing light levels (Boden and Kampa 1967). Since cephalopods migrate during twilight periods, light cues received by the vesicular organs may serve to trigger or regulate their migrations. This view is supported by three sources of evidence. First, nerves from the vesicles pass into the peduncle complex of the brain. Messenger (1967b) suggested, on the basis of experimental evidence in *Octopus*, that this complex is part of a visuomotor system: visual information from the eyes enables this complex to exercise control over locomotion. Secondly, experimental evidence on the function of the photosensitive vesicles in neritic *Octopus* strongly suggests that these organs regulate diurnal activity patterns (R. Houck pers. commun.). Finally, most migrating cephalopods have large vesicular organs positioned to detect downwelling light. The only exceptions are species of *Mastigoteuthis* and *Chiroteuthis*, whose migration patterns are not as distinct as in other species.

If dorsal and central organs function primarily in the detection of downwelling light, we may have a clue to the peculiar arrangement of vesicular organs in ommastrephids. The ommastrephids were the only squids that had central organs on the dorsal surface of the optic stalk as well as dorsal organs. In *Nototodarus hawaiiensis*, these two organs differ morphologically (the small central organ has large component vesicles and the large dorsal organ has small vesicles), but the organs are adjacent to one another. The structural differences suggest separate functions for the organs, yet their close proximity indicates that both will be exposed to the same source of light. The same argument holds for these organs in other ommastrephids, although the two organs are

somewhat further separated. The ommastrephids have the unusual habit of usually living in epipelagic waters but occasionally descending to great depths (Roper and Young 1975). Perhaps the central organs function in epipelagic waters while the dorsal organs operate only in deep water. Certainly there are considerable problems associated with a single organ functioning over such a wide range of light intensities.

Certain photosensitive vesicles appear to detect bioluminescent light rather than downwelling skylight. The small vesicular organs in the deep-living *Vampyroteuthis infernalis* are shielded from downwelling skylight (Young 1972a). Vesicular organs are present in the blind bathypelagic octopod *Cirrothauma murayi* (J. Z. Young in Packard 1972) which lives in depths where detectable surface light is absent. Certain photosensitive vesicles of many other species were shielded from downwelling light. Such organs presumably detect bioluminescent light. Young (1973, 1977) demonstrated that certain vesicular organs in some species were directly exposed to the animal's photophores, presumably for counterillumination purposes.

The detection of bioluminescence is not limited, however, to the animal's own photophores. With only a few exceptions all species examined had some means of "viewing" various parts of the mantle cavity with their vesicular organs. In many cases, the organs seemed precisely placed for this purpose (see Figure 6). In most species with large opaque livers (e.g., ommastrephids, enoploteuthids, histioteuthids, bathyteuthids, cycloteuthids, octopoteuthids, and mastigoteuthids), some organs extended laterally or ventrally past the liver, enabling a "view" of the mantle cavity. In other species with the liver far back in the mantle cavity (e.g., cranchiids, *Brachioteuthis*, *Ctenopteryx*), only central organs were present. In *Vampyroteuthis infernalis*, the organs lay within the mantle cavity and could only be exposed by light originating within this cavity, the funnel, or at the mantle opening. This animal, like most other cephalopods, had no photophores in these locations. The photosensitive vesicles in octopods were also located within the mantle cavity. The view of the mantle cavity is obscured only in *Onychoteuthis*, *Chiroteuthis*, *Joubiniteuthis*, and Chiroteuthidae gen. sp., although most of these species could still detect light from within the funnel and at the entrance to the mantle cavity.

Young (1972a) suggested that the photosensitive vesicles in *Vampyroteuthis* detect small glowing organisms that are carried into the mantle cavity with the respiratory current. In the deep sea, a glowing organism within the mantle cavity could reveal the squid's location and have disasterous consequences. J. Z. Young (1977) extended this idea to octopods. Nevertheless, this suggestion seems unlikely to have broad application in explaining the consistent relationships between vesicle location and mantle cavity "visibility"; however, no alternative function has been found.

Some squid may detect bioluminescent light originating outside the animal. The large vesicular organs in the deep-living *Bathyteuthis abyssicola* are not exposed to its own photophores and probably detect bioluminescence from animals located outside its restricted visual field (Young 1972a). In *Ctenopteryx siculus*, the elongate vesicular organs joined in the midventral line over the funnel and were there shielded dorsally and laterally by a thick layer of iridophores. The ventral part of this organ would detect light originating within the funnel. Yet, the high organization and sophisticated structure of the vesicles seem overly matched for such a task. This organ probably "looks" ventrally through the funnel to the area below the squid. Similar arguments could be made for certain lobes in other squids.

The photosensitive vesicles in many cephalopods apparently form an elaborate system for monitoring bioluminescent light from their own photophores, from within the mantle cavity, and from the immediate vicinity of the animal that lies outside the visual field

The great variety of photosensitive vesicles found among the species of pelagic cephalopods off Hawaii presumably reflects a variety of functions for these organs associated with the detection of both downwelling and bioluminescent light. The morphology and placement of these organs have provided some clues to these functions. A full understanding of this complex sensory system, however, must await experimental studies on living animals.

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Note added in proof: The correct name for the species listed here as *Phasmatopsis fisheri* is *Megalocranchia fisheri* (N. Voss. In press. Studies on the cephalopod family Cranchiidae. A revision of the genera, with a key for their determination. Bull. Mar. Sci.)