Transitory Eye Shapes and the Vertical Distribution of Two Midwater Squids[1]

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ABSTRACT: In two cranchiid squids, *Sandalops melancholicus* and *Taonius pavo*, the shapes of the eyes change with growth. Compressed eyes with ocular appendages occur in the larvae living in the upper few hundred meters of the ocean. Tubular eyes occur in juveniles that live within a depth zone between about 400 and 700 m. Nearly hemispherical eyes are found in adults living at depths greater than 700 m. The shapes of the compressed and tubular eyes offer strong countershading advantages to squids living at depths where downwelling light is important in prey–predator relationships.

MOST CEPHALOPODS have eyes that have a more-or-less hemispherical shape. In a number of pelagic cephalopods, however, the eyes exhibit various modifications of this shape. For example, the forward-looking eyes of *Bathyteuthis* are somewhat less than hemispherical; the eyes of the midwater octopus *Amphitretus pelagicus* are tubular; while the eyes of young *Sandalops melancholicus* and *"Doratopsis" lippula* are laterally compressed (Chun 1910, 1914). Modified shapes also occur widely in midwater fishes. For example, Marshall (1971) listed 11 families that have some members with tubular eyes.

Of the various ocular shapes in fishes and cephalopods, the tubular shape has been most widely discussed (e.g., Brauer 1908; Walls 1942; Munk 1966; Marshall 1954, 1971). A tubular eye is nearly cylindrical in shape and is stopped by a large lens at one end and by a thick retina at the other.

Munk (1966) demonstrated that the tubular eye corresponds to the central core of a hemispherical eye. Most authors (e.g., Walls 1942, Marshall 1971) have suggested (but not demonstrated) that the tubular eye corresponds to a large, hemispherical eye. Young (1975)

considered that the dimorphic eyes (one large semitubular eye and one small hemispherical eye) in squids of the family Histioteuthidae support this assumption.

In nearly all tubular-eyed animals the optical axes of the eyes are parallel or nearly parallel, allowing binocular vision. Advantages of binocular vision may be: better depth perception (Brauer 1908), lowered visual threshold (Weale 1955), and/or increased signal-to-noise ratio (Fremlin 1972).

The value of the tubular shape (as well as most of the other ocular shapes) remains unresolved, although Franz's (1907) suggestion that the tubular eye is merely a large eye in a compact form has considerable appeal (Munk 1966). One of the major obstacles in explaining the various ocular shapes has been the lack of reliable data on the habits and habitats of the animals involved.

In this report are examined two midwater squids that have eyes that change from compressed to tubular to nearly hemispherical as the animals grow. These ocular changes are correlated with changes in the depth distributions of the squids.

MATERIALS AND METHODS

All specimens were captured off the island of Oahu in the Hawaiian archipelago at approximately 158°20′ W, 21°20′ N over bottom depths from about 1,500 to 4,500 m. Two types of trawls were used: a modified 3-m

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Tucker trawl and a 3-m Isaacs-Kidd midwater trawl (IKMT). The Tucker trawl opens and closes at the fishing depth; hence specimens cannot be captured during setting and retrieving of the trawl. Because this trawl has a tendency to wander somewhat during fishing, the range as well as the principal fishing depth (usually the modal depth) is indicated in the distribution charts. The opening-closing mechanism utilizes a mechanical release activated by weighted messengers sent down the towing cable.

The IKMT is always open, and occasionally specimens are captured during the raising and lowering of the trawl. This contamination is minimized by dropping the trawl as rapidly as possible and retrieving it with the ship moving slowly ahead. The net is pulled horizontally at 3 to 4 knots. The modal depth of the net during the horizontal phase is assumed to be the depth of capture. Depth records for both trawls were obtained with a Benthos time–depth recorder.

One eye of *Sandalops melancholicus* was fixed in Bouin's solution in seawater and embedded in Epon 812 for sectioning. Sections approximately 2 μm thick were cut on a A.O. rotary microtome with a steel knife and stained with Richardson's stain.

Taonius pavo is especially prone to injury in the trawl and most specimens captured were badly damaged. As the eyes of the largest adults were damaged, the illustrations and description of the adult eye given here are based on a specimen of *T. pavo* that was captured in good condition off southern California. There seem to be no significant differences in the adults from these two localities. Measurements of retinal thickness in adult *Sandalops melancholicus* and all *Taonius pavo* were made from hand-cut aqueous mounts. These measurements are not very accurate and those presented are conservative.

RESULTS

Sandalops melancholicus Chun, 1906

LARVA (Figure 1*A*): The mantle is elongate (about three times as long as broad), thin-walled, and saccular. The posterior end of the larva has a characteristic appearance consisting of a broad, flat pen that tapers rapidly to a point, and of two pedunculate fins (Figure 2*A*). The fin insertion lies well in advance of the apex of the pen. The liver, with its associated ink sac, is spindle-shaped and covered by silvery iridophores.

The brachial crown is supported on a long, muscular stalk which can probably bend in any of several directions. In preservation, the brachial crown points anteriorly in young larvae, but tends to arch dorsally in older larvae. The arms are minute and the tentacles are long and robust. The larva is transparent except for the eyes and liver and bears a few chromatophores.

The eyes (Figure 2*B*, *C*) are located on long stalks and are laterally compressed. The length (dorsal–ventral) of the eye is about three times the lens diameter, while its width is only slightly greater than the lens diameter. The retina is likewise compressed into a broad dorsal-ventral strip, which is rounded at either end and slightly broader in the ventral half. I could not detect an iris.

Attached to the ventral surface of the eye is the ocular appendage—a cone-shaped projection of tissue with a thick layer of silvery iridophores. The rest of the eye, except for the dark dorsal surface, is covered with silver or green iridophores.

JUVENILE (Figures 1*B*, *C*; 2*D*, *E*): The thin-walled mantle is about three times as long as broad. The pen and small fins at the posterior end of the mantle retain the characteristic arrangement found in the larva. The arms are very small. The tentacles were broken off in all specimens; however, the remnants indicate comparatively robust tentacles. The normal position of the brachial crown appears to be tilted dorsally about 60° from the body axis. Although the muscular stalk of the brachial crown indicates that this structure is capable of some movement, two living but moribund individuals showed the dorsal tilt as did all preserved specimens. In contrast, the funnel maintains a typical orientation to the body axis. The juvenile is very transparent except for the eyes, the liver with its associated ink sac, and a few scattered chromatophores on the head and arms. The liver is long and spindle-shaped and
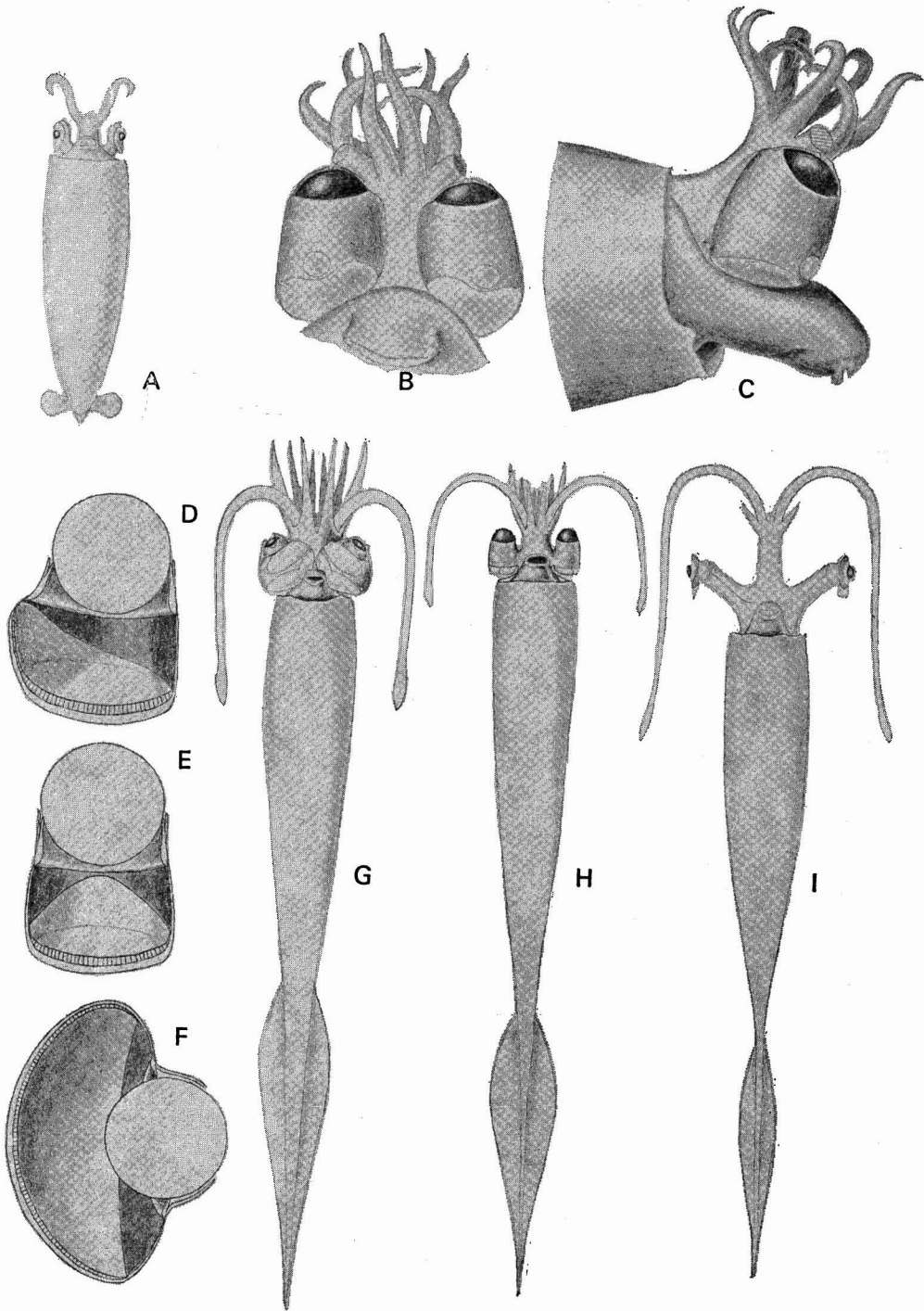
FIGURE 1. *A–C—Sandalops melancholicus:* *A*, ventral view of larva; *B*, anterior view of the juvenile head (camera lucida); *C*, lateral view of the juvenile head (camera lucida). *D–I—Taonius pavo:* *D*, cutaway lateral view of the tubular eye (reconstructed); *E*, cutaway anterior view of the tubular eye (reconstructed); *F*, cutaway lateral view of the adult hemispherical eye; *G*, ventral view of the adult; *H*, ventral view of the juvenile; *I*, ventral view of the larva.
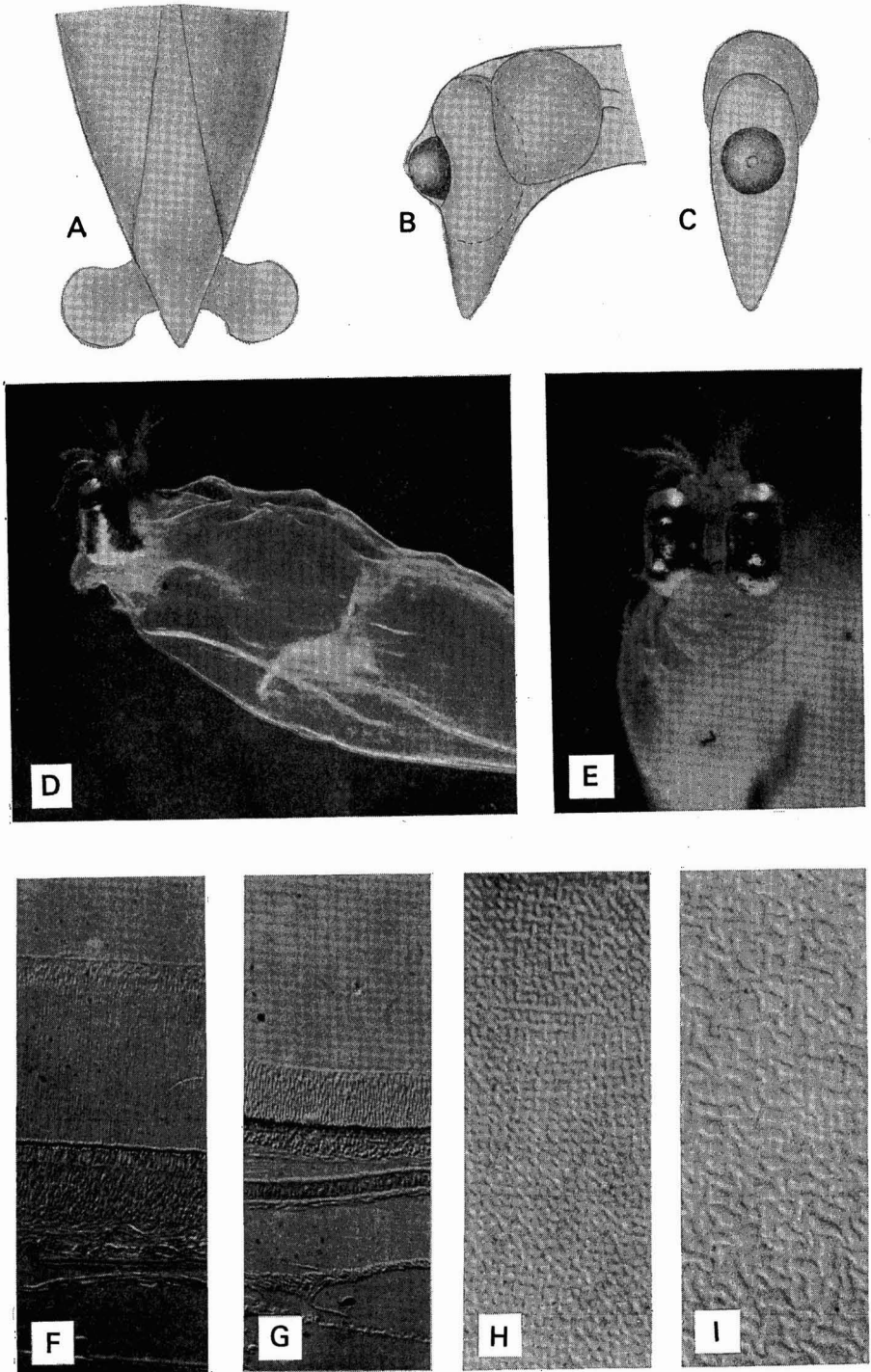
FIGURE 2. *Sandalops melancholicus*. *A*, dorsal view of the posterior end of the larva; *B*, lateral view of the larval eye; *C*, frontal view of the larval eye; *D*, anterior photograph of a moribund juvenile; *E*, lateral photograph of a moribund juvenile (orientation artificial); *F*, cross section of the main retina of a tubular eye; *G*, cross section of the accessory retina from the same tubular eye at identical magnification; *H*, frontal section of the main retina from the same tubular eye; *I*, frontal section of the accessory retina from the same tubular eye (magnification the same as in *H*). Photographs *F–I* were taken through a differential interference contrast microscope.
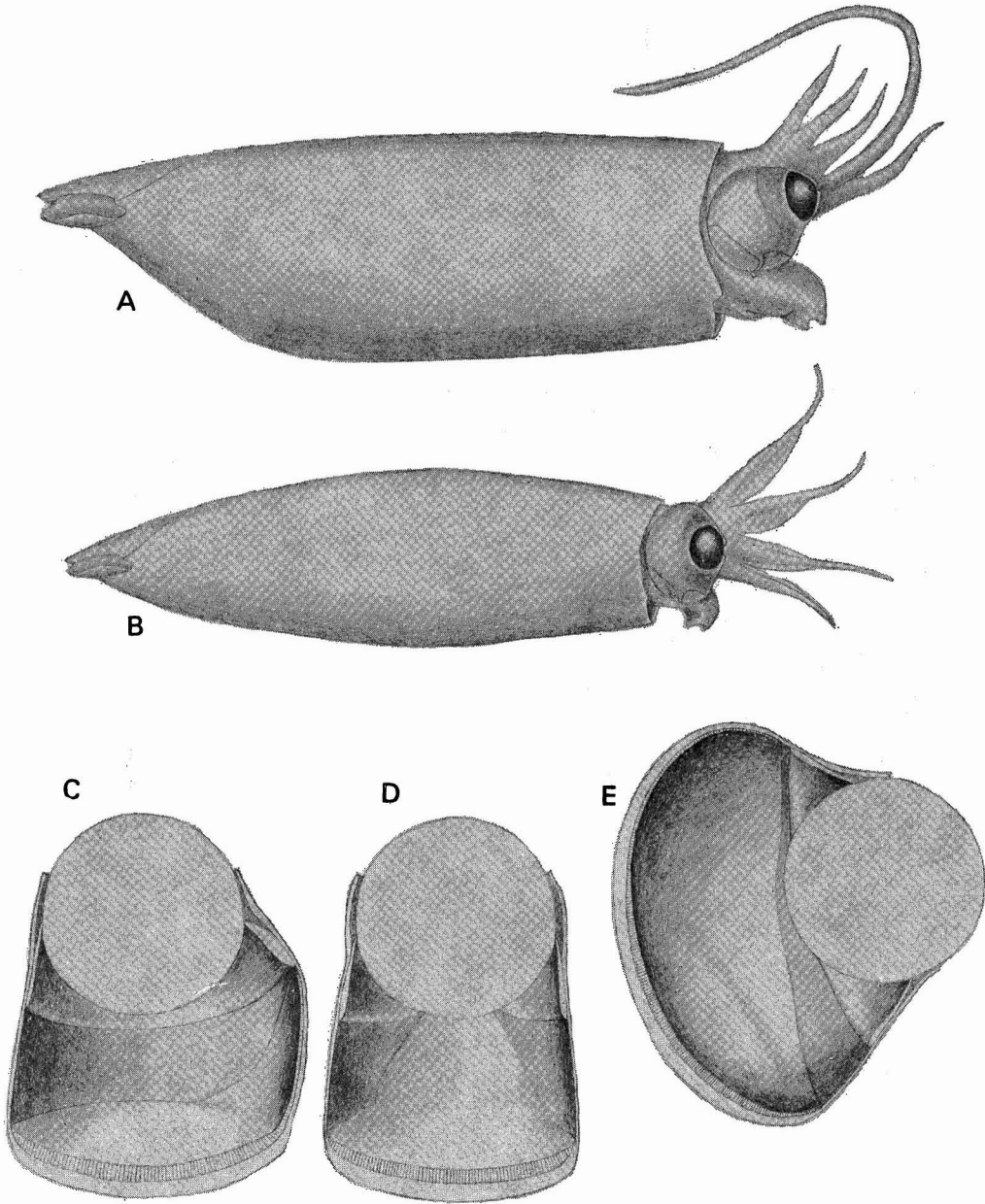
FIGURE 3. *Sandalops melancholicus*. *A*, lateral view of adult female (camera lucida); *B*, lateral view of adult male (camera lucida); *C*, cutaway lateral view of tubular eye (reconstructed); *D*, cutaway anterior view of tubular eye (reconstructed); *E*, cutaway lateral view of hemispherical eye of adult female (reconstructed).

is covered with iridophores which reflect gold to purple light.

The eyes are tubular (Figures 1*B*, *C*; 2*D*, *E*; 3*C*, *D*). Each, except for a bulge on the posterior wall, is a nearly straight-sided cylinder.

The walls consist of the pigmented epithelial body that supports the lens and a broad, heavily pigmented epithelial layer below. The retina consists of two portions: a thick main retina and a thin accessory retina. The main

retina occupies the circular base of the eye. Posteriorly it thins to become the accessory retina, which extends up the bulging mid-posterior wall of the eye from a broad base to a narrow rounded tip near the epithelial body (Figure 3C, D). Capture and fixation invariably result in considerable distortion of the eyes, preventing a precise measure of the distance between the accessory retina and the lens. However, the best determination indicates that nearly all of the accessory retina is too close to the lens for images to be in focus (see Figure 2E).

The distal segments (photosensitive processes) of the retinal cells of the main retina are long (290 μm), and slender (3–4 μm); they have a uniform cross-sectional shape and are regularly arranged (Figure 2F, H). In contrast, the distal segments of the retinal cells of the accessory retina are relatively short (90 μm) and broad (5–10 μm); they have an irregular cross section and are irregularly arranged (Figure 2G, I). Both retinas have a rather uniform thickness except for the narrow transitional region between them.

As in most squids, the muscular integument of the head covers the eyes and forms a circular eyelid around the lens. A very narrow iris leaves a broad pupil about the same diameter as the lens. The eyes are aligned parallel to each other and, along with the brachial crown, tilt strongly in a dorsal direction (about 60° from the body axis). The sides of the eyes, except where they attach to the head, are covered by iridophores reflecting purple to gold light. The bottom of the eye is covered by a large photophore which, except for an anterior indentation and a posterior bulge, is nearly circular. A second smaller photophore is situated in this indentation and extends up the anterior face of the eye. The reflective characteristics of both photophores indicate that they shine in the opposite direction to which the eye is facing.

Photophore development coincides with the transition of the eye from the larval form to the tubular form. Just prior to transition a large photophore appears on the proximal side of the ocular appendage. The appendage progressively shortens and, when only a remnant remains, the second, smaller ocular photophore appears on the distal face of the eye. Thus, what was

the apex of the appendage comes to lie between the two photophores of the tubular eye.

ADULT (Figure 3A, B): Two adults of *Sandalops melancholicus*, a mature male and an immature female, were captured. The mantles of these animals are broader at the anterior end than are those of the juveniles. The small posterior fins in each animal maintain their characteristic relationship to the broad terminal portion of the pen. The head and brachial crown are greatly enlarged relative to the juvenile condition. This is especially true in the male, where the arms are much longer and thicker than in the female. The brachial crown of the large female still has a slight dorsal tilt which is nearly absent in the male. In the male, the distal halves of arms I–III have no protective membranes, and the suckers are reduced to small knobs in numerous irregular rows. No trace of the tentacles remains in the male. In both specimens the liver is long and spindle-shaped and exhibits a trace of iridescence. The head and arms have a dense concentration of chromatophores. Since the outer integument of the mantle was missing in both specimens, I could not determine the mantle pigmentation.

The eyes in both specimens approach a hemispherical shape. Although the eye was damaged in the female, it appears to differ from a hemispherical eye only in being slightly compressed. The divisions of the retina found in the juvenile eye could still be detected (Figure 3E). A thick portion (distal segments about 240 μm long) is located in the ventral-posterior portion of the "visual" hemisphere and has a circular shape with about the same diameter as the lens. The rest of the retina is much thinner and covers most of the remaining surface of the "visual" hemisphere of the eye.

The retina of the adult male retains no trace of the tubular condition. Along the midline of the eye in a dorsal-ventral direction, most of the retina is thick with the central portion being slightly thicker. However, thin areas of the retina are present but are restricted to a narrow ribbon along the ventral margin and to the medial and lateral margins of the "visual" hemisphere with the dorsal areas being somewhat more extensive. In a dorsal-ventral section the shape of the eye is an almost perfect semi-
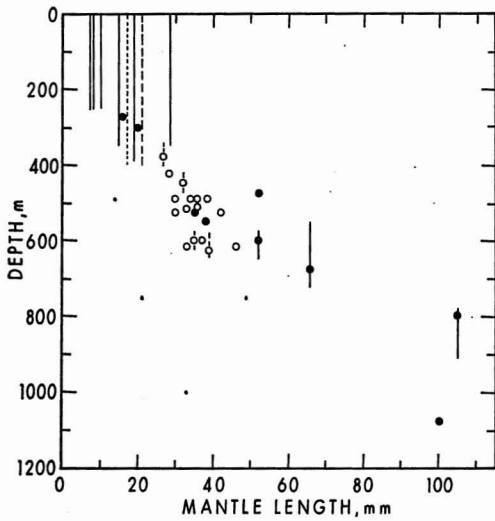
FIGURE 4. Vertical distribution of *Sandalops melancholicus*. Open circles represent day captures; closed circles represent night captures. A bar with a circle indicates an opening-closing tow with the bar representing the range of the tow and the circle the most likely depth of capture. A circle without a bar indicates a capture in an open tow. A bar without a circle indicates an oblique tow. Solid bars represent night captures. Bars with large dashes represent day captures. Bars with small dashes represent twilight captures. Small dots represent probable contaminants from open tows.

circle. In a lateral-medial section the eye is rather compressed, and much of the thinner retina may not be at the focal plane. The lens is surrounded by a narrow epithelial body and a large, wide, pigmented epithelium that is somewhat broader ventral to the lens.

Each eye in the female has a slight dorsal tilt and an anterior-lateral tilt from about 30° to 40° from the body axis. Therefore, the optical axes are no longer parallel but diverge some 60° to 80°. The eyes in the male, except for having a lesser dorsal tilt, show the same orientation. Both specimens have large heavily pigmented irises. The ocular photophores are greatly enlarged, with the larger of the two covering much of the posterior-ventral surface of each eye.

VERTICAL DISTRIBUTION: The 37 captures of *S. melancholicus* present a clear general picture of the vertical distribution of the species (Figure 4). Some interpretation of the data is necessary, however, as many specimens were taken in open nets. Because of the large amount of

midwater trawling that has been done in Hawaiian waters with open nets, the capture of some specimens (i.e., contaminants) during setting and retrieval of deep tows is expected. Four specimens are considered to be contaminants. Six specimens were captured in oblique tows, and their depth of capture within the depth range of each tow is unknown.

Day captures and night captures reveal no clear differences in depth distribution. Apparently, diel vertical migration does not occur. *Sandalops melancholicus* exhibits a clear pattern of ontogenetic descent in which progressively larger individuals occupy progressively greater depths. Correlated with these depth changes are changes in the morphology of the eyes.

VERTICAL DISTRIBUTION AND EYE STRUCTURE: Thirteen larval specimens of *S. melancholicus* of 28 mm mantle length (ML) or less have compressed eyes with ocular appendages, while one 28-mm specimen has eyes intermediate between the larval and the tubular conditions. All of the specimens with larval eyes (except two probable contaminants) were captured in the upper 400 m. The specimen with intermediate eyes was taken at 425 m. The twenty specimens of 30–52 mm ML probably captured between 450 and 625 m all have tubular eyes. The specimen of 66 mm ML captured probably at 675 m has eyes that have a tubular appearance but are somewhat more globular than the typical tubular eyes. The 105-mm ML specimen captured probably at 800 m was the adult female, and the 100-mm ML specimen captured at 1,075 m was the adult male; both have nearly hemispherical eyes.

Taonius pavo (LeSueur, 1821)

LARVA (Figure 1I): The mantle is thin walled and very long and attenuate. The liver is spindle shaped and has a golden metallic sheen. A muscular stalk supports the brachial crown. The arms are small, and the tentacles are long and robust. Except for the eyes, the liver and associated ink sac, and a few chromatophores, the larva is transparent.

A single larva with slightly damaged eyes was captured. The eyes are located on long stalks and seem to be identical in shape (i.e.,
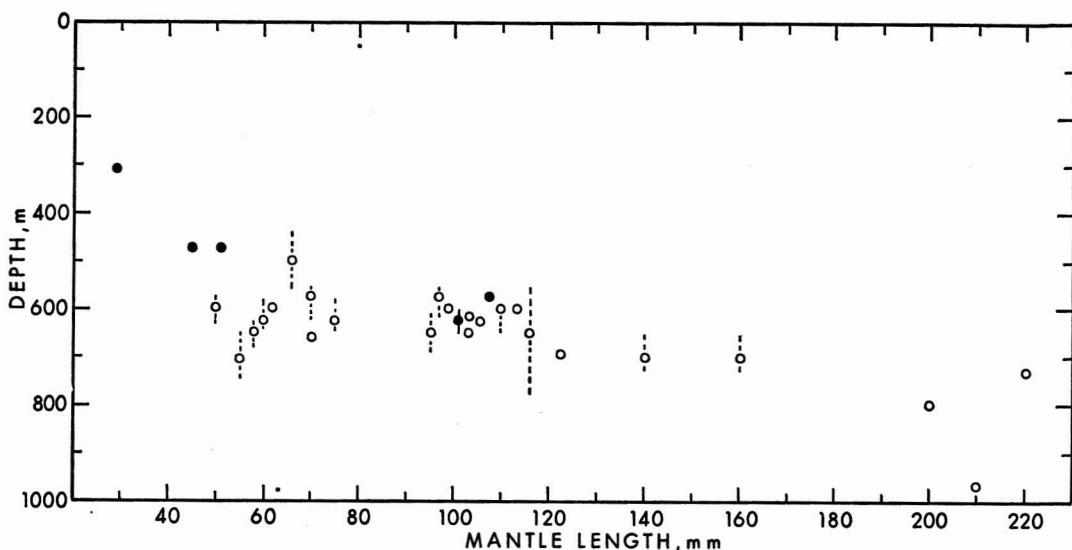
FIGURE 5. Vertical distribution of *Taonius pavo*. See legend to Figure 4 for explanation of symbols.

laterally compressed) to the eyes of larval *Sandalops*. The outer tissue has been lost from the eyeballs so no trace of ocular appendages remain. Because they probably do exist in undamaged eyes, I have included them in the drawing (Figure 1*I*) as dotted lines.

JUVENILE (Figure 1*H*): The mantle and fins are long and attenuate, and the mantle wall is thin. The liver with its associated ink sac is long and spindle shaped and is covered with a layer of purple iridophores. The tentacles are three to four times the length of the short arms. Scattered chromatophores are present in the mantle, funnel, head, and arms. With contracted chromatophores the living animal undoubtedly is very transparent.

The eyes are tubular (Figure 1*D*, *E*). Their walls, except for a bulge on the medial side, appear to be nearly cylindrical. The epithelial body forms the distal half of the cylinder; most of the remainder consists of heavily pigmented epithelium. The retina is divided into two portions: a thick main retina and a very thin accessory retina. The main retina, which occupies the circular base of the eye, has distal segments about 180 μm long. The accessory retina has a broad base which nearly encircles the main retina and extends up the medial wall

to a rounded apex beneath the epithelial body. The transition between the main and accessory retinas is more gradual than it is in *S. melancholicus*, and the accessory retina continues to thin toward its periphery; however, the distal segments over much of the accessory retina are 25–50 μm long or less.

The eyes appear to have parallel alignment, but this is uncertain due to damage. The iris is narrow, and the pupil is nearly the same diameter as the lens. The entire base of the eye is covered by two large, adjacent photophores, which together have a circular outline that covers the circular base of the eyes. The more posterior photophore has a broad V-shaped indentation into which the smaller, more anterior photophore fits. Although the eye had been damaged, portions of the thin covering remaining on the dorsal, ventral, and lateral surfaces of the eye have a purple metallic sheen.

ADULT (Figure 1*G*): The body shape of the adult is long and attentuate. The arms and tentacles are relatively larger than in the juvenile. The liver and its associated ink sac form a spindle-shaped structure which is dark brown and lacks any trace of iridescence. Chromatophores are densely concentrated on the head, arms, and mantle.

The adult eye of *Taonius* (Figure 1F) is almost perfectly hemispherical. A very narrow epithelial body surrounds the lens and a large, pigmented epithelium forms most of the distal wall of the eye. The pigmented epithelium is slightly broader ventral to the lens. The retina has the same thickness throughout except at its periphery, where it rapidly thins. The lengths of the distal segments of the retinal cells are about 290 μm. The photophores are greatly enlarged and cover most of the ventral hemisphere of the eye. Other than being present around the photophores, iridophores are not present on the eye. There is a large, heavily pigmented iris.

VERTICAL DISTRIBUTION: Vertical distribution based on 31 captures of *Taonius pavo* is presented in Figure 5. As with *Sandalops melancholicus*, some contamination (one 63-mm specimen placed at 980 m in Figure 5) apparently resulted from a capture during the setting or retrieval of the open IKMT. Another type of contamination seems to have occurred as well. A specimen entangled in the net may be washed into the cod-end collecting bucket in a subsequent tow. The IKMT net was not always carefully examined after each tow, and one anomalous capture (80-mm specimen at 50 m) may be a result of this type of contamination.

Although the data on larvae and adults are sparse, a pattern of ontogenetic descent appears to be present: larvae occur in the upper 400 m; most juveniles occur between 600 and 650 m, and larger juveniles and adults occur at 700 m or deeper. Other than one typical larva and two metamorphosing larvae, nearly all of the captures were made during the day. Most captures were made between 500 and 700 m, yet in this zone night sampling was over 60 percent as extensive as day sampling. Indeed, all depths above 800 m were well sampled at night. Since the squid probably do not descend into greater depths at night, they simply may be able to avoid the net better at that time. The capture depths of the few specimens taken at night, including one in an opening-closing tow, suggest that diel vertical migration does not occur.

VERTICAL DISTRIBUTION AND EYE STRUCTURE: The only specimen with larval eyes was cap-

tured at 310 m at night. Two specimens with stalked eyes partially transitional between the larval and the juvenile condition were captured at 475 m at night. Tubular-eyed juveniles from 50 to 140 mm ML were captured between 500 and 700 m, with most specimens (14 of 22 captures) being taken between 600 and 650 m. The eyes of the 160-mm specimen (captured at 700 m) were severely damaged and their shape could not be determined. The 220-mm and 200-mm specimens have adult hemispherical eyes, and the 210-mm specimen presumably had similar eyes; unfortunately the head of this specimen was missing. The latter animals came from depths of about 730, 800, and 965 m.

DISCUSSION

Vertical Distribution and Eye Shape

The larvae of *Sandalops melancholicus*, which live in relatively near-surface waters, have stalked, laterally compressed eyes that bear ocular appendages. Juveniles occupy greater depths and have tubular eyes with large ventral photophores, while adults occupy still greater depths and have eyes that approach the normal, hemispherical shape. Since there is little difference in the mantle length between large larvae and small juveniles, the transition from the larval eye to the tubular eye appears to be abrupt, occurring at a depth of 400 to 450 m. From the few specimens available, it appears that the transition from a tubular to a nearly hemispherical eye is more gradual. Tubular eyes are found in specimens captured as deep as 625 m. The initial stages of transformation to a hemispherical eye are found in a specimen captured near 675 m, while almost completely transformed adult eyes occur in the specimen captured near 800 m. If these two specimens are representative, then a gradual transformation in shape occurs in animals living between about 675 to 800 m.

The stalked larval eyes of *Taonius pavo* probably exhibit the same features as the larval eyes of *Sandalops melancholicus*. The evidence indicates that as larvae descend from relatively near-surface waters into the juvenile habitat (from about 500 to 700 m) the eyes transform into a tubular shape, and as juveniles descend

farther into the adult habitat (below 700 m) the eyes transform into a nearly hemispherical shape. The overlap in mantle length between the larvae with transitional eyes and the smallest juveniles suggests that as in *S. melancholicus* the transformation to tubular eyes is rapid. No evidence is available concerning the rate of transformation from the tubular to the hemispherical eye.

Off Hawaii nearly all captures of the semi-tubular-eyed squid *Histioteuthis dofleini* were also made in the 500–700 m depth zone (Young 1975). Apparently the tubular-eyed juveniles of *Sandalops melancholicus* and *Taonius pavo*, as well as the semitubular-eyed squid *Histioteuthis dofleini*, all live within a depth zone that extends from about 400 to 700 m in Hawaiian waters. Most tubular-eyed fishes off Hawaii are also restricted to these depths during the daytime (e.g., *Argyropelecus*, *Ichthyococcus*, *Opisthoproctus*, *Danaphos*) (T. Clarke and S. Amesbury, personal communication). Other tubular-eyed species (e.g., scopelarchids, evermannellids, giganturids) have ranges that extend well below these depths, and some (e.g., *Bathyleptus lisae*) exhibit peak abundances below 700 m. However, all of these deeper living tubular-eyed species have ranges that extend upward to about 500 m (T. Clarke and S. Amesbury, personal communication). The change in ocular shape in *Sandalops* and *Taonius* as they pass through these depths suggests that the tubular eye is an adaptation to this twilight zone.

The dwarf male angler fish of the family Linophrynidae, which have small, slightly downward-looking tubular eyes, are exceptions to this distribution pattern (see Bertelsen 1951). The size and orientation of the tubular eyes in these animals is also unusual. The eyes in male linophrynids, however, represent a special case of adaptation that bears little relationship to the present discussion.

Function of the Tubular Eye

EYE SIZE: I have compared the lens sizes of *Sandalops melancholicus* and *Phasmatopsis fisheri*, a cranchiid with large hemispherical eyes. Although precise comparisons are difficult to make, due to the somewhat different body

shapes, the lens sizes of *Sandalops melancholicus* are comparable to those of the large eyes of *Phasmatopsis fisheri*. In addition, although specimens for comparison are few, the lenses of the large adult eye of *Sandalops melancholicus* do appear to have about the same ratio to mantle length as do the lenses of the tubular eyes of the juveniles. The more elongate body in *Taonius pavo* prevents comparable measurements with *Phasmatopsis fisheri*. In *Sandalops* the tubular eyes correspond to the central core of large eyes, and the same is probably true for *Taonius*.

One probable function of large eyes is to increase visual sensitivity (Walls 1942). One might expect that the ultimate sensitivity of an eye would be limited by the sensitivity of the receptor cells. However, in humans the absorption of one photon will trigger a response in the retinal cell (Lewin 1972). If we assume this same sensitivity, together with efficient absorption, in deep-sea animals, the limiting factor may well be in the "noise" in the system, this noise perhaps being due to spontaneous breakdown of retinal pigment (see Denton and Warren 1957). If this is true, then to increase sensitivity the signal-to-noise ratio must be increased by the reduction of "noise."

Parts of the eye of *Sandalops melancholicus* may be modified to increase the signal-to-noise ratio. The main retina contains many long slender cells as compared to the accessory retina (Figure 2F–I). Slender cells may have a distinct advantage by increasing the signal-to-noise ratio. Although Walls (1942: 69) stated that bulky cells and extensive summation promote sensitivity, he also noted (p. 216) that in nocturnal animals the rods tend to be very slender and numerous. Denton and Warren (1957) and Denton (1959) have demonstrated that there is an increased density of visual pigment in the retinae of deep-sea fishes. If the spontaneous breakdown of visual pigment produces noise, then it would certainly be advantageous if the amount of pigment per cell in the retina was reduced while high overall retinal pigment densities were maintained. A bulky cell with a large quantity of pigment might be in danger of almost constant discharge. The smaller the amount of pigment in a cell, the greater is the chance that a cell dis-

charge will represent the absorption of a photon and not noise. Presumably a slender cell would carry less pigment than a broad cell of the same length. A possible elaboration of this system occurs in deep-sea fish with multiple layers of rod acromeres in their retinas. Many deep-sea fishes exhibit this condition, e.g., *Bathylagus benedicti*, *Winteria telescopa*, *Gonostoma elongatum*, *Bathophilus metallicus* (Munk 1966), although the overall thickness of the acromere zone is no greater than it is in species with elongated acromeres (Munk 1966). Presumably, the pigment per cell is very low in those species with multiple layers in the retina. The same argument holds for other possible sources of noise related in magnitude to cell size.

SHAPE OF THE JUVENILE AND ADULT EYES: In discussing the shape of the tubular eye, we must note that the direction that the eye normally faces in the water is of great importance. Unfortunately evidence concerning the body orientation of *S. melancholicus* and *T. pavo* is meager. Clarke, Denton, and Gilpin-Brown (1969) noted that *Helicocranchia pfefferi* floated in an aquarium with the head downward. I have also observed this head-down position in several species of young cranchiids. McSweeney (personal communication), on the other hand, noted that large specimens of the cranchiid *Crystalloteuthis glacialis* floated in the aquarium with the tail slightly downward. Unfortunately, no observations of juvenile *Taonius pavo* have been made in an aquarium and only inconclusive observations of juvenile *Sandalops melancholicus* are available. The specimens of *S. melancholicus* which I observed were dead or moribund and damaged. These specimens floated in a horizontal position. I suspect, however, that this squid could orient in almost any position with only the slightest effort.

A strong morphological clue to the normal orientation of *S. melancholicus* is provided by the large ocular photophores. Each eye bears a large, nearly circular photophore that almost covers the base of the tubular eye. A second, much smaller circular photophore lies partially within a small anterior notch of the large photophores on the anterior wall of each eye. These two photophores are properly positioned to produce a downward beam of light that would ventrally countershade each tubular eye if the eyes were directed vertically upward. In addition, the sides of the eyes bear a strong purple to gold metallic sheen that would be effective in countershading only if the eyes were oriented vertically. Further, the head tilts strongly in a dorsal direction (Figures 1C, 2D). This tilt is always present in preserved juveniles and seems to be a permanent and unique feature. Because of this strong dorsal tilt, the eyes can be directed vertically upward if the body is tilted only slightly from the horizontal or if the head is tilted somewhat farther while the body remains horizontal. In the photograph (Figure 2D) I have assumed that the former situation applies and have positioned and trimmed the photograph so that the eyes are directed vertically upward.

In contrast to *S. melancholicus*, the tubular eyes of *Taonius pavo* are directed anteriorly. Each eye carries two large photophores that precisely cover the base of the eye. Assuming these to be countershading photophores, as in *Sandalops melancholicus*, the eyes must be directed vertically upward. This interpretation is supported by the presence of iridophores on the ventral wall of the eye, which indicates a vertical rather than a horizontal orientation. As extensive rotation of the eyes is unlikely, the squid probably orients vertically with the head up and the tail down.

The tubular eyes in both of these species probably point vertically upward. Young (1975) has presented evidence for the same vertical orientation of the semitubular eye of the squid *Histioteuthis dofleini*. Indeed, the upward orientation probably applies to tubular-eyed fishes as well. In most midwater fishes with tubular eyes, the eyes are dorsally directed in species that probably orient horizontally (e.g., *Argyropelecus*, *Opisthoproctus*) and are anteriorly directed in species that may orient vertically (e.g., giganturids, *Stylephorus*), although there is little evidence from living animals to confirm this upward orientation.

Thus, tubular eyes occur in fishes and squids that are restricted to or, at least, that are occasional inhabitants of the twilight zone during the day. The eyes appear to be directed vertically upward. They probably represent large eyes in most species, and they usually

provide binocular vision. The possession of large, upward-looking eyes in species inhabiting the twilight zone is presumably related to the strong predominance of vertical downwelling light. But how are we to account for the fact that the eyes are tubular and not hemispherical? Large hemispherical eyes directed vertically upward would have all the advantages of tubular eyes and more. However, they would also have a severe disadvantage: they would bulge greatly from the sides of the head, resulting in a presumably awkward shape for a streamlined, fast moving fish or squid. As suggested by Franz (1907), the compactness of the tubular eye seems highly advantageous. However, for *Sandalops melancholicus* and *Taonius pavo*, compactness alone cannot explain the tubular shape of their eyes. These squids are quite capable of handling large bulging eyes, and, indeed, the adults have such eyes. I suggest that the tubular shape in this instance has the advantage of being easier to camouflage than an upward-directed hemispherical eye.

Many animals living in the twilight zone have some means of camouflage, generally through transparency or countershading. One of the most difficult problems in countershading is elimination of the ventral shadow. In some animals, this problem has been minimized by a small horizontal cross section. For example, *Argyropelecus* is very thin, and some snipe eels are long and slender and orient vertically (Barham 1971). Many animals in this zone apparently eliminate the ventral shadow by the production of a ventral bioluminescent glow (Clarke 1963).

Except for the eyes and the liver with its associated ink sac, juvenile *Taonius* and *Sandalops* are very transparent. Thus, only the eyes and liver-ink sac need to be countershaded. The area of the shadow cast by a tubular eye is less than 15 percent of a comparable-sized eye (i.e., same dioptric dimensions) of hemispherical shape. Further, the tubular shape with straight sides and flat bottom is more easily countershaded laterally and ventrally. The liver is long and spindle-shaped and presumably orients vertically, producing only a small shadow. Thus, the tubular-shaped eyes allow these squids to have large, upward-looking eyes that are easily camouflaged.

SHAPE OF THE LARVAL EYE: The ocular appendages on the eyes of larval *Sandalops* are not unique structures. Similar appendages are known in many cranchiid larvae (e.g., *Leachia*, *Helicocranchia*, *Bathothauma*, *Phasmatopsis*) and in the larvae of *Discoteuthis laciniosa* (Cyclotheutidae). They probably also occur in larval *Taonius*. John Z. Young (1970) examined these structures in detail in the larvae of *Bathothauma* and suggested that they might be photophores which emit light through an apical pore. Certainly in some species (e.g., *Leachia* spp.) the ocular appendages carry photophores on their outer surfaces. Whatever the role of these appendages in light production, their primary function probably is one of countershading.

Larval *Sandalops melancholicus* and probably larval *Taonius pavo* occur in the upper several hundred meters of water during the day, and the same is probably true for most other squid larvae that possess ocular appendages. With the exception of the eyes and liver-ink sac, these larvae are very transparent. The eyes of *Sandalops melancholicus* and probably *Taonius pavo* are countershaded laterally and distally with mirrorlike iridophores and dorsally with dark pigment. Because of the high ambient light intensities the eyes cannot be countershaded ventrally with bioluminescent light. Other techniques must be utilized. The compressed shape of the larval eye, with the resulting reduced horizontal cross-sectional area, lessens the extent of the shadow. Denton and Nicol (1965) have demonstrated that the presence in some fish of a ventral keel that bears silvery sides can greatly reduce the shadow region below the fish. The ocular appendages appear to be simply silvery keels on the eyes. The liver of these animals is countershaded in a similar fashion through its long spindlelike shape and reflecting iridophores. The compressed eye suffers from a loss of lateral vision; however, the greater mobility of the eyes provided by the long stalks may compensate for this loss.

These specializations of the liver and eyes to reduce the ventral shadow would be meaningless if these organs did not maintain a vertical orientation in the water. I have made some preliminary observations on living larval *Phasmatopsis fisheri* in a shipboard aquarium. (This squid belongs to the same family as *Sandalops*

melancholicus and *Taonius pavo*). In this species the eyes and liver have the characteristic modifications, and, indeed, they maintain a constant orientation with their long axes vertical whether the animal is tilted upward or downward.

It thus appears that the compressed shape and ocular appendages of the larval eye and the tubular shape of the juvenile eye in these squids have evolved primarily for countershading purposes.

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