

Function of the Dimorphic Eyes in the Midwater Squid *Histioteuthis dofleini*¹

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ABSTRACT: The squid *Histioteuthis dofleini*, like other members of the family Histioteuthidae, has a large left eye and a small right eye. The large eye points in a dorsal posterior direction while the squid typically orients at an oblique angle with the arms downward. The large eye, as a result, points vertically upward. The small eye appears to be directed ventrolaterally. This squid occurs primarily at depths of 500 to 700 m during the day where it is exposed to low levels of downwelling light. Presumably the large eye utilizes this faint downwelling light while the smaller eye utilizes bioluminescent light.

SQUIDS of the family Histioteuthidae exhibit a peculiar modification of the visual system. During the larval stage, the eyes are normal in size and shape. At the termination of the larval period, the left eye becomes atypical in shape and rapidly enlarges relative to the right eye, the diameter becoming nearly twice that of the right eye in juveniles and adults. Two theories attempt to explain this peculiar development. Voss (1967; Lane 1960: 110) suggested that the large eye functions when the animal is in the dimly lit waters of the deep sea, whereas the normal eye functions in near-surface waters. Denton and Warren (1968) suggested the exact opposite; that the large eye is adapted for vision in near-surface waters, and the small eye for vision in deep waters. This idea, which is based on the presence of pigments in the lens of the large eye which absorb ultraviolet radiation, will be examined at the conclusion of this paper. Voss's suggestion that the large eye is an adaptation to the deep-sea habitat seems quite possible.

The value of a large eye to a deep-sea squid could be to increase visual sensitivity and/or visual acuity. Compared to a small eye, a large eye with a large retinal area may possess a greater number of visual cells and thereby

produce a less "grainy" image. Walls (1942: 210) stated, however, that in nocturnal vertebrates an enlarged eye is designed for greater sensitivity rather than for resolution. Indeed, one of the primary means of attaining high sensitivity (retinal summation) is achieved at the sacrifice of acuity. The large eye may provide a compromise between acuity and sensitivity as apparently happens in geckos, *Sphenodon*, and possibly owls (Walls 1942: 206), but little can be said on this subject at present.

Eye size in fishes and squids has only a marginal effect on the intensity of the retinal image due to the fixed relationship between the size of the lens and the focal length of the eye. The spherical lens is the only refractive structure in the eye (the cornea, when present, plays no role in focusing), and the lens shape cannot be altered. The refractive index of the lens, which is graded from the core to the periphery, is constantly readjusted with growth such that the size of the lens remains the only factor affecting focal length (Pumphrey 1961). This fixed relationship of lens size to focal length (retinal distance) is known as Matthiessen's ratio (the distance from the center of the lens to the retina is 2.55 times the radius of the lens). Walls (1942: 211) pointed out that, in such an eye, doubling the eye diameter would double the diameter of the retinal image. Thus, while more light is admitted in a large eye, it is spread over a larger retina so that illumination of the retina per unit area remains the same. However, Denton and

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Warren (1957) and Clarke and Denton (1962) stated that, for seeing small spots of light, a large eye has an advantage. This advantage holds for point sources of light that will be focused on single retinal cells and for small spots of light where the "grain" size of the retina becomes important. Thus, a large eye with a retinal image covering an area four times that of a smaller eye will have an increased retinal intensity if the image falls on less than four retinal cells. Therefore, while the retinal intensity of small spots or points of light viewed by the eye is affected by eye size, the retinal intensity of larger objects viewed by the eye is independent of the eye size.

A large eye with a greater number of retinal cells, however, has a distinct advantage over a small eye in increasing sensitivity through retinal summation. An all-rod vertebrate eye can increase sensitivity about one millionfold during dark adaptation, and one of the two most important mechanisms involved is retinal summation (Tansley 1965). The high degree of retinal summation in nocturnal vertebrates (Tansley 1965: 51) further supports the importance of this mechanism. Unfortunately, it is not known whether or not retinal summation occurs in cephalopods. If it does occur, it will take place in the optic lobes (perhaps in the "deep retina") where the axons from the retinal cells terminate. The complex structure of these lobes prevents the detection of summation with simple anatomical techniques. Whatever the mechanisms involved, it does appear that a large eye in a midwater squid would probably be very advantageous in, at least, increasing visual sensitivity.

If the large eye is an adaptation to the poorly lighted waters of the deep sea and the small eye to the well-lighted surface waters, then knowledge of the precise habitats of these squids could provide strong supporting evidence. The little information presently available on their habitats (Voss 1969; Roper and Young, in press), however, tends to contradict such a relationship.

During a study of the vertical distribution of pelagic cephalopods off Oahu, Hawaii, I have reexamined this problem based on information obtained on the vertical distribution and general biology of one species, *Histioteuthis dofleini*.

MATERIALS AND METHODS

All specimens were captured off the island of Oahu in the Hawaiian archipelago at approximately 158°18' W, 21°23' N over bottom depths of 1,500 to 4,500 m. Two types of trawls were used: a modified 3-meter Tucker trawl and a 3-meter Isaacs-Kidd midwater trawl (IKMT). The Tucker trawl opens and closes at the fishing depth; hence, capture of specimens during setting and retrieval of the trawl (contamination) cannot occur. The opening-closing mechanism utilizes a mechanical release that is activated by weighted messengers sent down the towing cable.

The IKMT is always open, and occasionally specimens are captured while the trawl is being raised and lowered. 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. Depth records for both trawls were obtained with a Benthos time-depth recorder.

RESULTS

Description of Histioteuthis dofleini

Histioteuthis dofleini is similar in appearance to other members of the Histioteuthidae except that the arms are relatively long and the mantle small. The photophores of *H. dofleini* exhibit a somewhat unusual distribution and orientation for a midwater animal. The precise arrangement of these light organs is important to the subsequent discussion. On the mantle, large photophores are concentrated on the anterior-ventral surface, with smaller and fewer photophores on the posterior and dorsal surfaces. On the ventral surface of the head, large photophores are closely spaced and evenly distributed except for the left side, ventral and posterior to the large eye, where they are lacking. The lateral portions of the head anterior to the eyes also bear large photophores. The dorsal surface of the head bears, for the most part, only a few small photophores. Seven large photophores are present near, but not at, the anterior-ventral edge of the large left eyelid, whereas the smaller right eyelid possesses 17 large photophores tightly packed

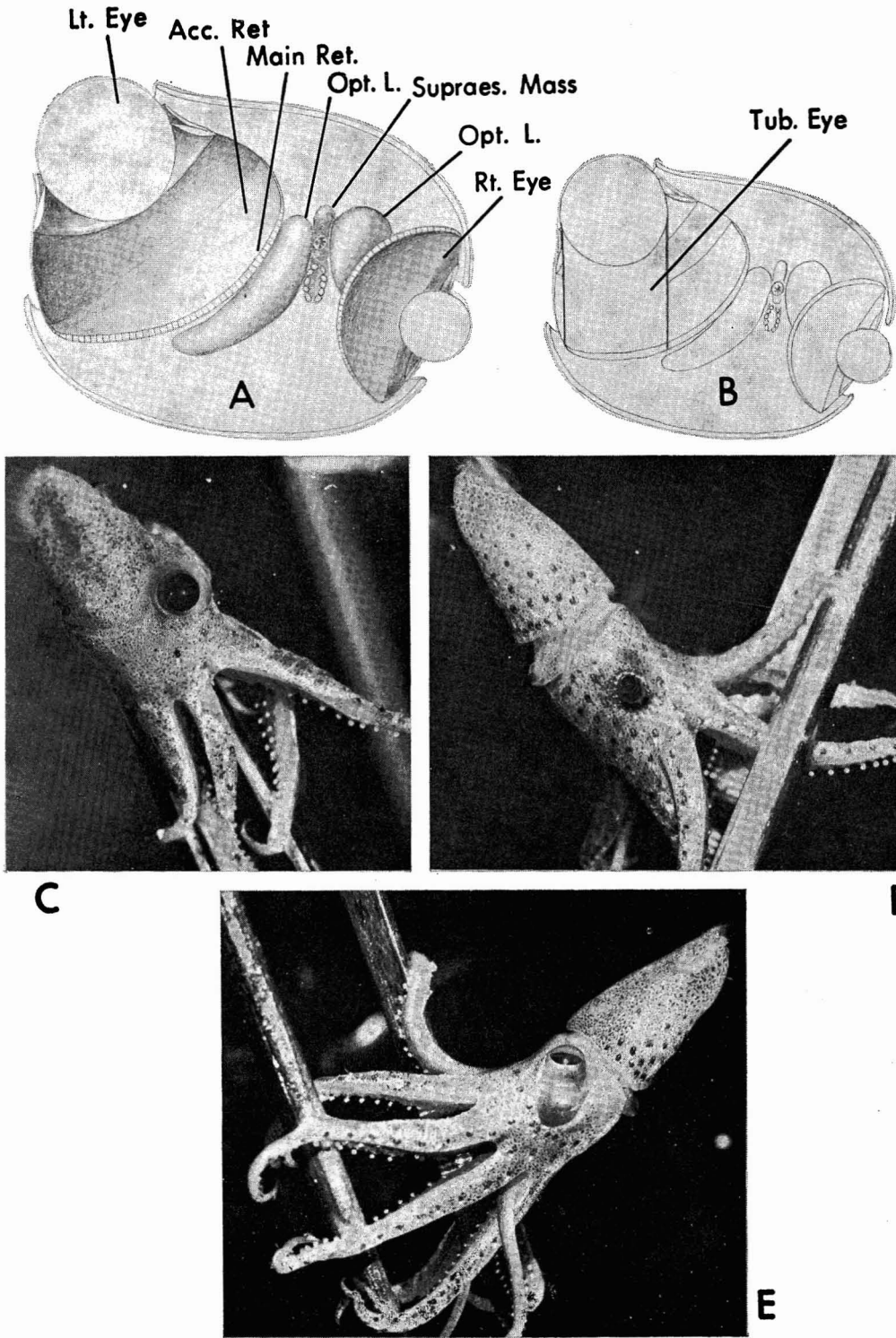


FIGURE 1. *Histioteuthis dofleini*. A, oblique section of the head of *H. dofleini* passing through the visual axes of both eyes; B, outline of the drawing in A but with the outline of a tubular eye superimposed on the large left eye; C, dorsal-posterior view of *H. dofleini* in an aquarium; this view is presumably what one would see if one were looking vertically downward at a specimen floating in the water; D, lateral view showing the small right eye; E, lateral view showing the large left eye. The object in the photographs with the squid is a pair of 12-inch forceps.

ABBREVIATIONS: Lt. eye, left eye; Acc. Ret., accessory retina; Main Ret., main retina; Opt. L., optic lobe; Supraes. Mass, supraesophageal mass; Rt. Eye, right eye; and Tub. Eye, tubular eye.

along the entire circular edge of the eyelid. The arrangement of reflectors and pigment on these latter photophores indicates that light from them does not enter the eye but passes anteriorly and somewhat laterally. Large photophores are found on the aboral surfaces of all four pairs of arms, although they are most numerous on the fourth (ventral) arms and least numerous on the first (dorsal) arms. All of the photophores face anteriorly. The skin of *H. dofleini* contains many reddish brown chromatophores that can greatly alter the color of the animal. When the chromatophores contract, the animal looks silvery due to underlying iridophores; and when the chromatophores expand the animal becomes deep brownish red. Chromatophores can also expand over the silvery tissue of the photophores. The iridescent layer is most prominent on the ventral and lateral surfaces of the head, the anterior surface of the mantle, and the aboral surfaces of the arms. A weaker layer is present on the dorsal surfaces of the head. Very little, if any, iridescent tissue exists on the dorsal and posterior surfaces of the mantle.

The right and left eyes differ greatly from one another in size and shape (Figure 1A). The right eye has a typical hemispherical shape and a spherical lens. It differs from a typical squid eye primarily in the structure of the retina. The dorsal-posterior portion of the retina is noticeably thicker than the anterior-ventral portion. The change in thickness is gradual, with the thickest portion being in the dorsal-posterior third and the thinnest in the anterior-ventral third.

The spherical lens of the left eye has twice the diameter of the right one. In absolute terms, the size of this eye is equally impressive. In a specimen of only 75 mm mantle length, the lens diameter is 15 mm. The eye does not have a hemispherical shape but has more the shape of a truncated cone with a curved base. The retina is divided into two portions of different thicknesses. The main retina (thick portion) is circular, nearly all of it being confined to the curved base of the cone and leaving most of the converging region of the eye free of any retina. The accessory retina (thin portion) is continuous with the main retina on all sides, but covers a much broader area

posterior-dorsally to the main retina than anterior-ventrally (Figure 1A). Because the eye is easily distorted by contraction of the head muscles during capture and fixation, it is not certain whether the accessory retina lies at the same distance from the lens as the main retina or whether it is closer to the lens, as illustrated in Figure 1A, B.

The orientation of the large left eye is atypical. Instead of the usual lateral orientation, the eye faces in a posterior-dorsal direction. It is probably capable of limited movement. In a living specimen of *H. heteropsis* off California I have observed the large eye move from a posterior-dorsal direction to a dorsal direction. Undistorted dead specimens of *H. dofleini* invariably have this eye directed posterior-dorsally, which is undoubtedly its more typical position. Because of the eye's orientation and large size, the head bulges laterally and the margin of the eyelid is elliptical and very large, passing around the lens and the lateral wall of the bulbus of the eye. This lateral portion of the eye that is not covered by the eyelid contains a layer of iridophores.

Vertical Distribution

The vertical distribution of *H. dofleini* is presented in Figure 2. The symbols in the figure require some explanation. Tucker trawl captures are represented by a vertical bar that indicates the total range fished by the net while it was open. Within this range the net usually fishes predominately within a narrow zone, the midpoint of which is indicated by a dot. The IKMT also fishes primarily within a narrow vertical range. The total range, of course, extends to the surface and, therefore, is not represented in Figure 2. The probable depth of capture is determined from the horizontal phase of the tow in the same manner as for captures from the Tucker trawl. Every IKMT tow below 700 m during the day and below about 300 m at night passes through the habitat of most of the population while the net is being set and retrieved. In such circumstances, some contamination is expected. I have assumed that five specimens (represented by the small dots in the figure) were captured in this fashion.

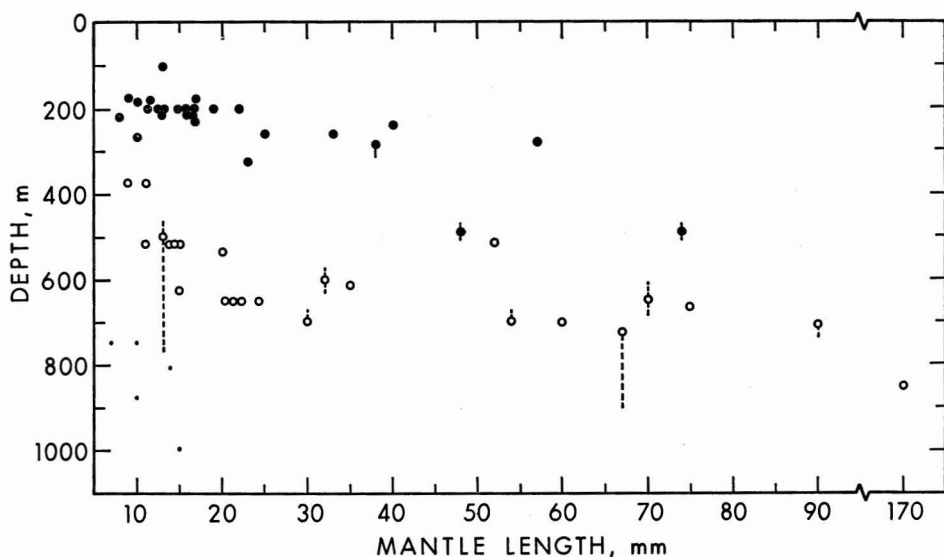


FIGURE 2. Vertical distribution of *Histiotenthis dofleini* off Hawaii. Each symbol represents a single capture. Large solid circle = depth of night captures; large open circles = depth of day captures; broken bars = depth range of opening-closing day tows; solid bars = depth range of opening-closing night tows; small solid circles = presumed contaminants.

The figure indicates that this species exhibits a diel vertical migration, moving upward several hundred meters at night. During both the day and night, the larger animals occupy progressively greater depths.

DISCUSSION

The vertical distribution of *H. dofleini* clearly indicates that its dimorphic eyes are not adaptations to habitats with greatly differing light intensities. Although this animal occurs in different day and night habitats, both habitats are characterized by very low light levels.

The daytime habitat of most *H. dofleini* is a zone of low light intensity, yet a zone where light plays a critical role in the ecology of many of the inhabitants. This twilight zone from about 400- to 700-m depth off Hawaii corresponds to the habitat of most half-red shrimp (Foxton 1970; J. Walters, personal communication), to the habitat of most animals bearing complex ventral photophores (Foxton 1970, Young 1973) and to the habitat of most fish (T. Clarke, personal communication; S. Amesbury, personal communication)

and squid (Young 1975) with tubular eyes. Although larvae of *H. dofleini* live well above the twilight zone in near-surface waters and larger adults are found in the lower reaches of the twilight zone or occasionally below it, most juveniles and young adults occur within it and exhibit characteristics typical of many squid living there, i.e., a layer of silvery iridophores overlain by functional chromatophores, and complex ventral photophores.

Within this zone the intensity of downwelling light is over one hundred times greater than that passing upward (see Tyler and Preisendorfer 1962: 423). Determining the typical orientation of *H. dofleini* within this strongly directional radiance pattern is critical to understanding the functions of the eyes. Clarke, Denton, and Gilpin-Brown (1969) have shown that a closely related squid, *H. reversa*, is neutrally buoyant. *H. dofleini* also appears to be nearly neutrally buoyant in an aquarium. Although the animal tends to rotate to a position with the mantle downward when motionless, it is probably capable of orienting in almost any direction with only a slight assist from the fins and funnel. The normal orientation of this species can be

deduced from the distribution of photophores on the head, mantle, and arms. These photophores point in an anterior-ventral direction relative to the longitudinal axis of the body. If the photophores are used in ventral counter-shading (i.e., elimination of the silhouette when viewed against the downwelling surface light), as are similar photophores in many other midwater animals (Clarke 1963; Foxton 1970; Denton, Gilpin-Brown, and Wright 1972; Young 1973), they then must be directed downward. In order to direct the photophores downward the squid must be positioned with the body axis at an angle of about 45° from the horizontal with the mantle uppermost. In this orientation the large eye looks upward in the direction of maximum light intensity.

The large eye of *H. dofleini* approaches a tubular eye in shape and has certain functional relationships to tubular eyes. In nearly all tubular-eyed species, the eyes seem to be directed either dorsally on a horizontally positioned animal (e.g., *Opisthoproctus*) or anteriorly on a presumably vertically oriented animal (most species with anteriorly directed eyes may orient vertically, as has been indicated for *Gigantura* and *Stylephorus* [Bruun 1957]). However, the fish *Winteria* may be an exception. Unfortunately the evidence concerning orientation in midwater animals is meagre.) The large histioteuthid eye is also directed upward and its visual field completely includes the vertical visual field of a tubular eye; yet, unlike the tubular eye, it maintains a broad lateral field of view (Figure 1B).

The probable function of a tubular eye has been examined by Munk (1966) and others. Munk demonstrated that the tubular eye is equivalent to the central core of a hemispherical eye. Fishes and cephalopods with tubular eyes have the optical axes of their eyes parallel or nearly parallel. The compact configuration of the tubular eyes facilitates the parallel orientation and thus binocular vision. Brauer (1908) suggested that binocular vision results in better judgment of distances, whereas Weale (1955) suggested that it results in lowering of the visual threshold. (Pirenne [1967] stated that binocular vision lowers the visual threshold in humans by 20 percent.) Fremlin (1972) suggested that binocular vision may increase

the ability to see details above the visual threshold by increasing the signal-to-noise ratio; actual retinal stimulation ("signal") could be distinguished from fluctuations in cell activity (noise) by analyzing retinal stimulation coincident on the two retinas.

Although most authors (e.g., Walls 1942, Tansley 1965) have suggested that tubular eyes represent large eyes, i.e., they correspond to the central cores of large eyes, this has not been rigorously demonstrated. The tubular eyes in fishes and cephalopods could represent the reduction of normal-sized eyes into compact spaces for parallel alignment and binocular vision. However, the semitubular eye of *H. dofleini* is clearly not just a normal-sized eye in a somewhat compact form. Rather it is nearly twice the size of its right counterpart. The arrangement in *H. dofleini* demonstrates the problem of having large upward-directed eyes. Even though the eye does not have the full normal shape in this species, it still grossly distorts a very large head. By analogy, this arrangement in *Histioteuthis* suggests that tubular eyes of fish are indeed large eyes in a compact form designed for viewing the vertically downwelling light, and that binocularity, therefore, is not the only factor involved.

The small eye of *H. dofleini* has an anterior tilt. An additional ventral tilt results from the tilt of the head imposed by the large right eye. This latter tilt also explains the asymmetrical arrangement of the photophores on the ventral surface of the head. When the animal is in its presumed typical orientation, the small eye tilts slightly downward. Therefore, while the large and presumably more sensitive eye points upward in the direction of maximum light intensity, the smaller eye, directed laterally and ventrally, points in a direction of very low light intensity. The latter eye probably receives less than 5 percent of the downwelling illumination that the upward-looking eye receives (see Tyler and Preisendorfer 1962: 423). These circumstances suggest that, whereas the large upward-looking eye detects downwelling surface light, the small eye does not; rather, it detects bioluminescent light. Further, the compact arrangement of photophores around the smaller eye, combined with the modifications of the retina, suggests that counter-

shading is not the only function of these organs. These ocular photophores are ideally located to produce a strong beam of light that would illuminate the portion of the environment that is surveyed by the thicker portions of the retina. In other words, these photophores may function as a searchlight.

Lens Pigments

Denton and Warren (1968) suggested that the large eye of *Histioteuthis* functions in near-surface waters because of the light-absorbing characteristics of the lens. They found that in *H. meleagroteuthis* the lens of the small eye is transparent to light down to about 310 nm, whereas the lens of the large eye always absorbs the near ultraviolet and sometimes blue light. These authors pointed out that such features are characteristic of surface-dwelling fishes and squids. However, catch records demonstrate that *Histioteuthis* spp. do not normally occur in near-surface waters during the day-time and the previous discussion has attempted to demonstrate that the large eye is adapted for vision under conditions of low light intensity. In near-surface species, an ultraviolet-absorbing lens may protect the retina from damage (Denton and Warren 1968) or may improve visual acuity by reducing chromatic aberration (Wald and Griffin 1947). The reason for the ultraviolet-absorbing pigments in the large lens of *Histioteuthis* remains a mystery.

SUMMARY

1. *Histioteuthis dofleini* lives primarily in the twilight zone (approximately 400 to 700 m depth) during the day and migrates upward several hundred meters at night.
2. This squid has a large left eye with a semi-tubular shape and a small right eye with a typical hemispherical shape.
3. *H. dofleini* probably orients at an oblique angle in the water so that the large eye is directed vertically upward while the small eye is directed ventral-laterally.
4. The disparity in the size of the two eyes suggests that tubular eyes in other mid-water animals are indeed enlarged eyes, as

has been previously suggested by several authors.

5. The small right eye may function primarily in the detection of bioluminescent light and the photophores that surround the lens may function as a searchlight.
6. The large left eye functions primarily during the day in detecting downwelling light.

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