

# TOPOGRAPHICAL DISTRIBUTION OF VISUAL CELL NUCLEI IN THE RETINA IN RELATION TO THE HABITAT OF FIVE SPECIES OF DECAPODIFORMES (CEPHALOPODA)

AKIHIKO MAKINO AND TAEKO MIYAZAKI

Graduate School of Bioresources, Mie University, Kurima-machiya-cho, Tsu, Mie 514-8507, Japan

Correspondence: T. Miyazaki; e-mail: taeko@bio.mie-u.ac.jp

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## ABSTRACT

Studies of retinal histology of fish have established that the position of an area of high cell density reflects both the habitat and feeding behaviour. Here, we discuss potential relationships between biology, specifically behaviour and ecology, and visual axes (estimated from density of visual cell nuclei) in five species of Decapodiformes. In all species, the posterior retina had the highest cell density. In coastal species, the region of highest density was dorsal to the midline of the body, meaning that the visual axis was likely directed downwards and forwards, suitable for focusing on the sea bottom. In oceanic species, the highest density region was ventral to the midline, meaning that the visual axis was directed upwards and forwards. This may be advantageous for detecting prey silhouetted against light from above in the open ocean.

## INTRODUCTION

Decapodiform cephalopod species have a well-developed camera-type eye, which evolved independently from that of vertebrates (Nilsson, 2004). Previous studies of aspects of vision in decapodiform species have included retinal structure (Zonana, 1961), the type of visual pigment (Hara & Hara, 1965; Michinomae *et al.*, 1994), and sequence and spectral tuning of visual pigment (Bellingham, Morris & Hunt, 1998). Cephalopods have a remarkably high level of visual acuity, similar to that of vertebrates (Messenger, 1981; Muntz & Gwyther, 1988), they have a visual contrast threshold superior to that of fishes (Siriraksophon, Nakamura & Matsuike, 1995), great sensitivity to the orientation of polarization of incoming light (Saidel, Lettvin & Macnichol, 1983; Shashar, Rutledge & Cronin, 1996; Shashar *et al.*, 2000; Mäthger & Denton, 2001; Cronin *et al.*, 2003) and widely divergent visual axes combined with highly mobile eyes (Schaeffel, Murphy & Howland, 1999).

Similarities of visual ability and function between cephalopods and fish suggest that cephalopod retinas and eyes may mirror the diversity documented among fishes. For example, in fish vision, cone photoreceptor arrangement and/or topography of retinal ganglion cells (RGCs) across the whole retina often reflect species-specific feeding behaviour and/or habitat (Collin & Pettigrew, 1988a, b; Williamson & Keast, 1988; Browman *et al.*, 1990; Beaudet, Flamarique & Hawryshyn, 1997). Collin & Pettigrew (1988a, b) compared the iso-density contour maps of RGCs in 10 teleost species from different reef habitats. The fishes, whether living in enclosed environments (e.g. caves or densely vegetated coral zones) or open water, shared the greatest density of RGCs in the temporal retina; in species from open water, dense RGCs also extended horizontally across the retinal meridian. Fishes from enclosed habitats are ambush hunters, whereas open-water fishes must keep watch for predators. The temporal peak in RGCs in both fish groups is presumed to allow binocular vision while feeding in front of the animal; the strong horizontal streak in open-water fishes may enhance their ability to detect predators elsewhere in the visual environment.

The cephalopod retina is comparatively simple, being essentially composed of a single cell type, the retinal cell (or retinula cell or rhabdomere), a photoreceptor analogous to the cone and rod photoreceptors in vertebrates (Young, 1962). Retinal cells are arranged in groups of four to form a rhabdome (Young, 1971), the functional unit of the cephalopod retina. Rhabdomes are oriented in both vertical and horizontal planes, allowing the organism to perceive polarized light. While retinal variation has been noted among species (Young, 1962, 1963), few studies have related these differences to habitat. Young (1963) measured rhabdome size, length and the numbers of nuclei of retinal and other cells across the retina in the cuttlefish, *Sepia officinalis*, and the nearshore squid, *Loligo pealeii*, demonstrating a clear difference in the arrangement of these retinal cells. A well-marked posterior fovea, with the longest rhabdomes, found only in *Sepia officinalis*, was suggested to relate to the direction of the most frequent visual stimulation in their coastal life. Its absence in *L. pealeii* was related to the squid's habit of swimming in shallow and well-illuminated water as shoals, looking backwards and forwards equally (Young, 1963).

This study investigates the density of retinal-cell nuclei across the whole retina in two coastal and three oceanic squid species, to document any differences in area or position of the region of highest cell density. Previous studies (e.g. Young, 1962) have determined that in Decapodiformes the visual transduction processes are conducted in the optic lobe, so that the retinal cell nuclei are not a 'bottleneck' in the visual system as the RGCs are in fishes (Land & Nilsson, 2002). However, to produce the retinal topographic maps, we adopted retinal cell nuclei, allowing us to assign the histological sections to specific locations in the retina.

Analysis of density of retinal cell nuclei across the retina found that coastal species have the area of highest density on the dorsal posterior retina, while oceanic species have the area of highest density on the ventral posterior retina. Based on these maps of retinal cell density, correlations between direction of visual axis, visual field and species-specific behaviour and habitat are discussed.

MATERIAL AND METHODS

Organisms

An eye from one individual from two coastal [*Euprymna morsei* (Verrill, 1881) (Sepioidae), *Sepioteuthis lessoniana* Férussac, in Lesson 1830–1831 (Loliginidae)] and three oceanic species [*Todarodes pacificus* (Steenstrup, 1880), *Eucleoteuthis luminosa* (Sasaki, 1915) (Ommastrephidae) and *Thysanoteuthis rhombus* Troschel, 1857 (Thysanoteuthidae)] were examined (Table 1).

The *Euprymna morsei* specimen was trawled at Hibiki-nada off the coast of Shimonoseki-city, Yamaguchi prefecture at night in October 2006. The *Sepioteuthis lessoniana* specimen was obtained by fishing at Owase-bay, Mie prefecture, in daytime during November 2005. The *Todarodes pacificus*, *Eucleoteuthis luminosa* and *Thysanoteuthis rhombus* specimens were jigged offshore of Kumano-nada, Mie prefecture, on board the T/S *Seisui-Maru*, Mie University, at night in November 2005. Immediately after capture, each sample was decapitated and the head fixed in Bouin's fluid.

Retinal histology

The right eyeball of each specimen was removed from the head, after making an incision in the anterior side of the iris to mark the direction of the eyeball. After removal of the iris, lens, sclera and optic nerve, each retina was flattened by making peripheral incisions. The retinas were scanned using a flatbed computer scanner (CanoScan-FB636U, Canon), and the images traced and contours drawn using Microsoft Office PowerPoint 2003. The retinas were then divided into five or six pieces, and further cut into 64–302 5-mm square pieces (Table 1). The positions of these retinal pieces were mapped back onto the original retinal contour drawing. We followed the method used for cone photoreceptor density mapping in fish (Miyazaki *et al.*, 2008) for retinal histology. Retinal pieces were dehydrated in an ethanol series and embedded in paraffin. Serial sections were cut tangentially at a thickness of 5 µm and stretched onto glass slides. These sections were then deparaffinised with xylene, dehydrated in an ethanol series and stained with haematoxylin and eosin. After clearing with xylene, sections were mounted in EUKITT (O. Kindler GmbH and Co., Germany).

Using a light microscope, we observed the deeper layer of the inner segment of serial sections, because retinal cell nuclei lie slightly deeper than supporting cell nuclei (Young, 1962). We counted all the recognizable nuclei of this layer per 0.25 × 0.25 mm (using an ocular micrometer) and converted counts to cells/square millimetre. Because the counts may have included a number of other cell nuclei (supporting cells and epithelial cells) these densities represent upper limits. The densities of the 64–302 points sampled in each retina were used to build iso-density contour maps of the cell nuclei for each species by connecting isopycnic points with a smooth curve.

Counting the rhabdome mosaic structures (equivalents of cone photoreceptors in fishes) was difficult in our paraffin preparations.

Our use of only one individual for each species is a shortcoming in our experimental design. Our two counts of *Euprymna morsei* and *Todarodes pacificus*, however, differed by <3% cell density with no change in the position of highest density.

RESULTS

Topographical distributions of cell nuclei across the whole retina differed among the species considered. Cell density was higher in centre of the retina and lower peripherally in all species, except *Eucleoteuthis luminosa* (Fig. 1). In *Eucleoteuthis luminosa*, the density peaked at the periphery of the retina, with cells being sparse near its centre (Fig. 1D). The highest density region was in the posterior retina in all species. This region was slightly dorsal to the midline of the body in *Euprymna morsei* and *Sepioteuthis lessoniana* (Fig. 1A, B), but ventral to the midline in *Todarodes pacificus*, *Eucleoteuthis luminosa* and *Thysanoteuthis rhombus* (Fig. 1C–E).

In teleosts, the visual axis is generally defined as the direction linking the centre of the lens and the retinal positions with the highest cell density (Tamura, 1957). Applying this definition to our work, we estimated the visual axes of *Euprymna morsei* and *Sepioteuthis lessoniana* to be directed downwards and forwards when observed from the lateral side (i.e. in the pitch plane) (Fig. 2-1A, -1B). In *Todarodes pacificus*, *Eucleoteuthis luminosa* and *Thysanoteuthis rhombus*, the visual axes were estimated to be upward and forward (Fig. 2-1C–E). In the horizontal plane, we presumed the visual axis of *Eucleoteuthis luminosa* to be directed almost forward because the highest cell density was located in the peripheral retina (Fig. 2-2D). For *Euprymna morsei*, *Sepioteuthis lessoniana*, *Todarodes pacificus* and *Thysanoteuthis rhombus*, all having the highest cell density region around the central retina, the visual axis was considered to be directed laterally (Fig. 2-2A–C, -2E). However, squids almost always hold a slightly downward posture while swimming or hovering (Mäthger, 2003), so their visual axes are correspondingly depressed (Fig. 2, Column 3). We therefore estimated that the visual axes of *Euprymna morsei* and *Sepioteuthis lessoniana* were directed downwards and forwards (Fig. 2-3A, -3B).

The density of cell nuclei was higher in the oceanic species than in the coastal species; the greatest density was in *Eucleoteuthis luminosa* (between 42,080 and 79,600 cells/mm<sup>2</sup>) (Table 1).

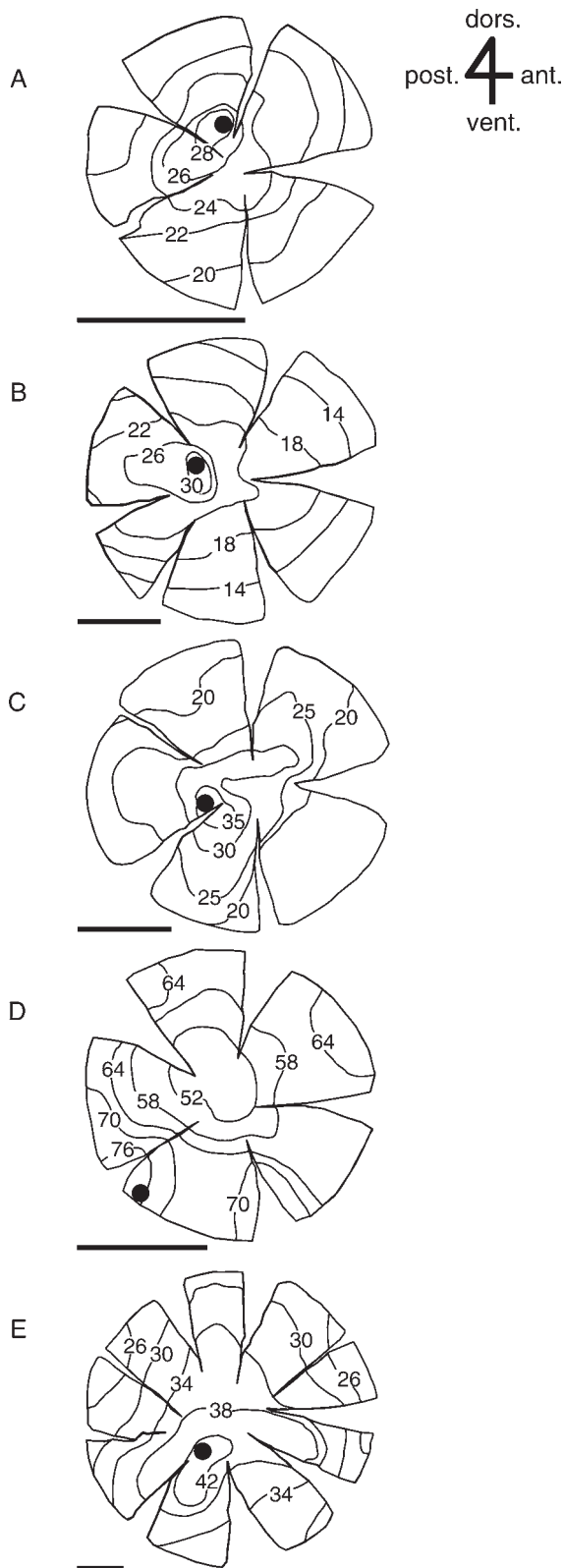
DISCUSSION

Visual axis in the pitch plane

The typically benthic bobtail squid *Euprymna morsei* feeds on small benthic crustaceans (Carpenter & Niem, 1998); its

**Table 1.** Summary of the habitat and visual cell nucleus density of five species of Decapodiformes.

Species (family)	Mantle length (mm)	Habitat	No. of retinal pieces	Density of visual cell nucleus (cells/mm <sup>2</sup> )		Lens diameter (mm)
				Maximum	Minimum	
<i>Euprymna morsei</i> (Sepioidae)	29	Coastal	64	28,640	17,840	5.07
<i>Sepioteuthis lessoniana</i> (Loliginidae)	180	Coastal	133	32,080	11,920	9.57
<i>Todarodes pacificus</i> (Ommastrephidae)	235	Oceanic	81	40,840	18,320	8.52
<i>Eucleoteuthis luminosa</i> (Ommastrephidae)	154	Oceanic	77	79,600	42,080	8.63
<i>Thysanoteuthis rhombus</i> (Thysanoteuthidae)	330	Oceanic	302	44,800	23,600	17.28



**Figure 1.** Iso-density contour maps of retinal cell nuclei for five species of Decapodiformes. **A.** *Euprymna morsei*. **B.** *Sepioteuthis lessoniana*. **C.** *Todarodes pacificus*. **D.** *Eucleoteuthis luminosa*. **E.** *Thysanoteuthis rhombus*. The bullet indicates the position of highest cell density. Density units =  $\times 10^4$  cells/mm<sup>2</sup>. Scale bar = 10 mm. Abbreviations: ant., anterior; post., posterior; dors., dorsal; vent., ventral.

downward- and forward-directed visual axis may enhance its ability to forage for prey. The visual axis of the cuttlefish, *Sepia officinalis*, which also has a diet based on benthic crustaceans (Pinczon du Sel, Blanc & Daguzan, 2000), is directed downward and forward during usual swimming or hovering. In contrast, nearshore squids *Sepioteuthis lessoniana* are considered to generally take pelagic prey, not being attracted to dead bait on the sea bottom (Segawa, 1993). At present we cannot relate their downward-forward visual axes to their feeding. Nevertheless, both our coastal species and *Sepia officinalis* studied by Young (1963) live near the sea bottom, and their lower frontal visual axes may be specialized to inspect the sea floor.

The oceanic squids mostly feed on mesopelagic organisms including small fishes, cephalopods and crustaceans (Packard, 1972; Ivanovic & Brunetti, 1994; Mouat, Collins & Pompert, 2001; Markaida & Sosa-Nishizaki, 2003; Watanabe *et al.*, 2004). In those considered here, *Todarodes pacificus* and *Thysanoteuthis rhombus* are estimated to have visual axes in the pitch plane directed almost completely forward (Fig. 2-3C, -3E), and in *Eucleoteuthis luminosa* it is directed forward and upward (Fig. 2-3D). As their feeding likely depends on vision, this upper frontal visual axis might be advantageous in detecting prey items in the open water, silhouetted by light from above. The attraction of squid to the light of the vessel (or to prey attracted by the vessel's light) in squid-jigging fishery is consistent with this hypothesis. Furthermore, in *Eucleoteuthis luminosa*, with the highest density of visual cells (Table 1), the upper frontal visual axis may pertain to the ability to detect ventral light organs of conspecifics (see below).

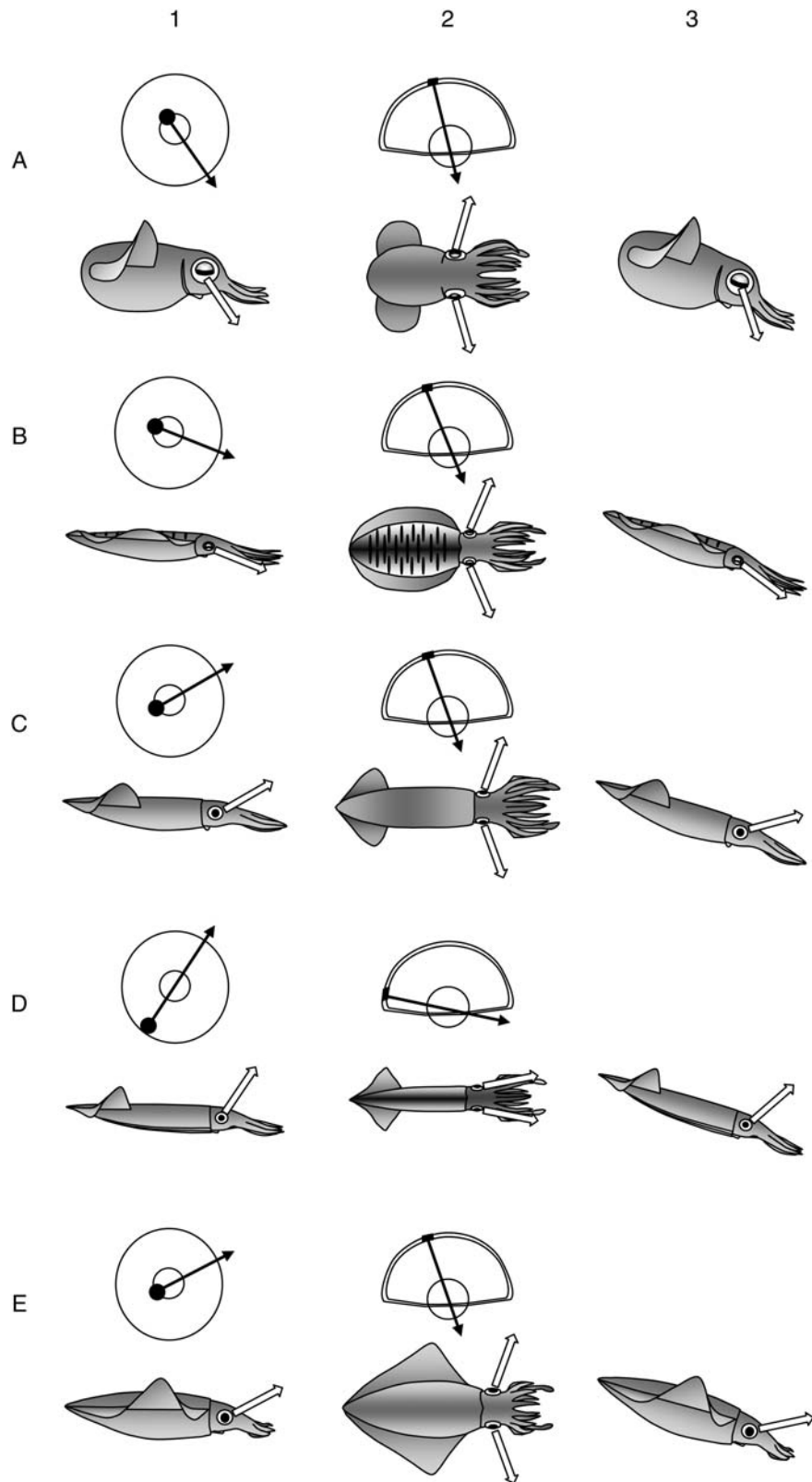
#### *Visual axis in the horizontal plane*

The visual axes in the horizontal plane were directed laterally and forwards in all five species. Although their monocular vision extends to almost 180° laterally, accuracy of attack on prey items may be significantly lower using monocular rather than binocular vision (Messenger, 1977). The lateral position of the eyes in squid may appear to limit binocular overlap, but well-developed extra-ocular muscles (Budelmann & Young, 1993) give the eyes high mobility and the lenses can move in any direction perpendicular to the papillary axis (Schaeffel *et al.*, 1999). Their excellent, if temporary, binocular vision enhances their judgement of distance and enables prey capture in the frontal field using their tentacles (Messenger, 1968, 1977; Budelmann & Young, 1993). We must conclude that our diagrams of the visual axes in the horizontal plane (Fig. 2, Column 2) only show the best monocular axes that may contribute to prey search by both eyes rather than prey capture.

#### *Visual acuity*

In fish, higher visual acuity relates to larger lens radius and higher retinal cell density. Although body size differs among the five species, our results showed that the lens is particularly large in *Thysanoteuthis rhombus*, while cell density of *Eucleoteuthis luminosa* is two to three times higher than that of the other four species (Table 1). Young (1963) reported cell density in the posterior central retina of the cuttlefish, *Sepia officinalis*, and the nearshore squid, *Loligo pealeii*, to be 104,000 and 51,000 cells/mm<sup>2</sup>, respectively. These results are comparable to our own (maximum densities 28,640–79,600 cells/mm<sup>2</sup>).

Schaeffel *et al.* (1999) attempted to calculate the anatomical resolving power of an adult cuttlefish using the average inter-rhabdome spacing (millimetre) and the posterior nodal distance ( $=2.55 \times$  lens radius, in mm) (using data from Heidermanns, 1928), by applying the equation used by



**Figure 2.** Schematic diagrams indicating visual axes estimated from the positions of highest cell density. **A.** *Euprymna morsei*. **B.** *Sepioteuthis lessoniana*. **C.** *Todarodes pacificus*. **D.** *Eucleoteuthis luminosa*. **E.** *Thysanoteuthis rhombus*. **Column 1.** Upper: schematic diagrams of the highest density positions (bullet) in the retina. The images were traced from Figure 1. Lower: the estimated visual axes (white arrows) when decapodiforms are observed from the lateral side (i.e. in the pitch plane). **Column 2.** Upper: schematic diagrams of the highest density positions (black dot) in the dorsal view of the eyecups. The positions were estimated based on Figure 1, by determining the distance of the highest-density position from the posterior edge relative to the equator line. Lower: the estimated visual axes (white arrows) when decapodiforms are observed from the dorsal side (i.e. in the horizontal plane). **Column 3.** Schematic diagram of visual axes (white arrow) when decapodiforms are in usual swimming or hovering posture.



Reymond (1985) to examine spatial acuity of an eagle. This calculation gave a value of 19.1 cycles/degree. To calculate visual acuity using density of visual cell nuclei and lens diameter, the equation of Collin & Pettigrew (1989) would be more applicable. This gives values of 9.5, 19.1, 19.2, 27.1 and 40.7 cycles/degree for *Euprymna morsei*, *Sepioteuthis lessoniana*, *Todarodes pacificus*, *Eucloteuthis luminosa* and *Thysanoteuthis rhombus*, respectively.

Among the five species we examined, *Thysanoteuthis rhombus* has the highest visual acuity; this large, highly vagile, oceanic species may therefore recognize distant objects. We consider, however, that the visual accuracy of this species is low because the large eye is liable to induce motion blur and lower its resolution due to its long focal distance (Land & Nilsson, 2002). On the other hand, the small, nearshore sepiolid, *Eucloteuthis luminosa*, may detect a target within their visual range with high accuracy, due to its small eye and high visual cell density. Warrant & Locket (2004) suggested that bathypelagic deep-sea fishes have surprisingly well-developed foveae that are superbly adapted to localize points of bioluminescence. To detect accurately a visual target or a point source like bioluminescence, the retina needs not only fine photoreceptor distribution, but the lens must also be able to provide high resolution. Although the lens resolution of *Eucloteuthis luminosa* is unknown, the eye of this species may have specializations to detect bioluminescence by conspecifics.

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## RETINAL CELL DENSITY OF SQUID

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