

Comparative visual acuity of coleoid cephalopods

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Synopsis The pelagic realm of the ocean is characterized by extremely clear water and a lack of surfaces. Adaptations to the visual ecology of this environment include transparency, fluorescence, bioluminescence, and deep red or black pigmentation. While the signals that pelagic organisms send are increasingly well-understood, the optical capabilities of their viewers, especially for predators with camera-like vision such as fish and squid, are almost unknown. Aquatic camera-like vision is characterized by a spherical lens focusing an image on the retina. Here, we measured the resolving power of the lenses of eight species of pelagic cephalopods to obtain an approximation of their visual capabilities. We did this by focusing a standard resolution target through dissected lenses and calculating their modulation transfer functions. The modulation transfer function (MTF) is the single most complete expression of the resolving capabilities of a lens. Since the optical and retinal capabilities of an eye are generally well-matched, we considered our measurements of cephalopod lens MTF to be a good proxy for their visual capabilities *in vivo*. In general, squid have optical capabilities comparable to other organisms generally assumed to have good vision, such as fish and birds. Surprisingly, the optical capability of the eye of *Vampyroteuthis infernalis* rivals that of humans.

Introduction

The deep pelagic realm of the ocean, the water column between ~200 m and the ocean floor, is the most voluminous habitat on earth. The ecology of the pelagic realm is dominated by long-range (tens of meters) visual interactions, as attested by the elaborate bioluminescent photophores, pigmentation, fluorescence, and well-developed eyes possessed by many of the species living there (Warrant and Locket 2004; Haddock et al. 2005). Contrary to popular belief, this part of the ocean is not empty water, but instead an often dense, soupy mix of detailed animal interactions. However, because most of the animals in this habitat have fragile, gelatinous bodies, they are difficult and expensive to collect, and impossible to maintain in the laboratory, little is known about their basic biology. Most pelagic species can only be studied on research vessels, and even then under conditions very different from the 3D, surfaceless environment they inhabit. Therefore, researchers have only half-jokingly described research on mesopelagic organisms as “forensic.” Animals from this vast and important habitat are often collected in a less-than-pristine condition, and then measured to the best of the researcher’s ability on a ship. Attempts are then made to extrapolate these ship-board measurements to the animals’ abilities *in vivo*.

Therefore, measurements of the visual capabilities of these animals can yield insights about otherwise unstudyable aspects of their *in situ* ecology, such as predation, evasive behaviors, and courtship and mating behaviors (Warrant and Locket 2004; Johnsen 2005).

Many researchers have studied aspects of vision in mesopelagic and bathypelagic waters (Frank and Case 1988; Lindsay et al. 1999; Frank 2000). Almost all of this work, however, has focused on the compound eyes of pelagic crustaceans, since both the eyes and vital organs of these animals usually remain intact when collected using mid-water trawling methods. Very little is known about the visual capabilities of pelagic organisms with camera-like eyes. Since these animals lack an arthropod exoskeleton, they are usually gelatinous and fragile. Even fish die soon after being brought to the surface and their lenses seem especially susceptible to cataract. Animals with camera eyes are also usually less common in trawls, and when caught, their eyes are easily damaged by abrasion. These factors have made it difficult to study camera-like vision in pelagic organisms. Many of these animals, however, especially squid, are also likely to be the top predators in this environment, making an understanding of their visual capabilities essential

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to a complete understanding of pelagic ecology. To our knowledge, only one other nonbehavioral study addresses the optical properties of squid lenses, although the methodology of this article is very different, and estimates the longitudinal chromatic aberration of the firefly squid *Watasenia scintillans* (Kröger and Gislén 2004).

The most complete single expression of the resolving capabilities of a lens is the modulation transfer function (MTF). It is a way of quantifying the decrease in contrast of black and white line pairs produced by a given lens as the spacing of those line pairs decreases. Numerically, it is the attenuation of contrast as a function of spatial frequency ν and is expressed as:

$$MTF(\nu) = \left| \frac{C(\nu)}{C_0(\nu)} \right| \quad (1)$$

where, $C_0(\nu)$ and $C(\nu)$ are the original contrast of an image and the contrast after passing through a given optical system (in this case, a lens). Contrast can be defined in several ways; for the test targets used in this study, it is defined as:

$$C = \frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}} \quad (2)$$

where, L_{\max} and L_{\min} are the maximal and minimal radiance of the test pattern at a given spatial frequency.

In the absence of the ability to perform behavioral experiments on an organism to determine its visual capabilities, the MTF of the lens represents a good opportunity to estimate them. The neural and optical capabilities of an eye are often well-matched, and in cases where they are not, the retina and not the lens is the limiting factor in vision (Frisen and Glansholm 1975; Seyer 1994; Artal et al. 1998; Coletta et al. 2003; Nilsson et al. 2005).

Materials and methods

Animal collection

Squid used in this study (Fig. 1) were collected from depths ranging from 50 to 1000 m in the eastern temperate Pacific Ocean and Gulf of California on several cruises of the *R/V Western Flyer* and the *R/V New Horizon* between November 2005 and October 2006. Squid from the *R/V Western Flyer* were collected using the remotely-operated vehicle *Tiburón*, and squid from the *R/V New Horizon* were collected using a Tucker trawl (Childress et al. 1978) with a closing, insulated cod end, as well as line-and-lure techniques (jigging) from the surface. The current study was possible due to collection

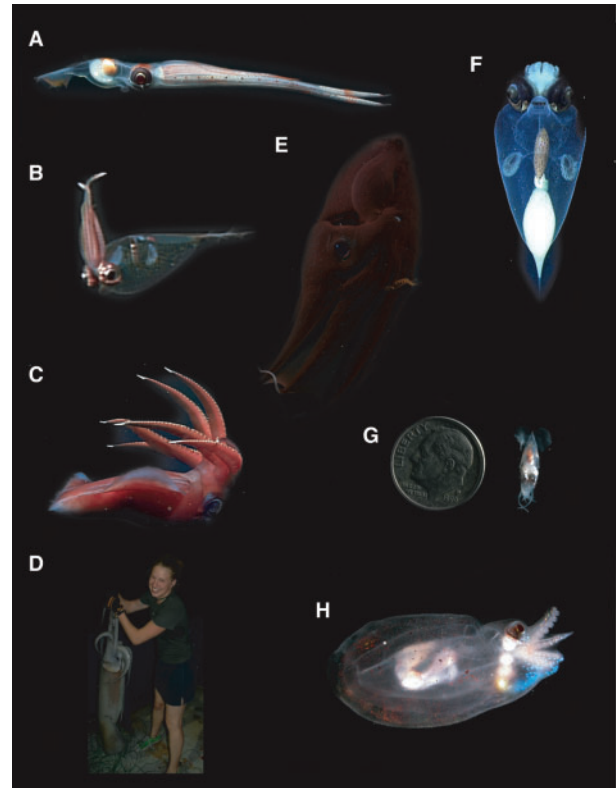


Fig. 1 Mesopelagic squid in this study and typical mantle length of specimens used in this study. (A) *Chiroteuthis* sp., 4 cm; (B) *Galiteuthis* sp., 6 cm; (C) *Octopoteuthis* sp., 8 cm; (D) *Dosidicus gigas*, 40–70 cm; (E) *Vampyroteuthis infernalis*, 8 cm; (F) *Helicocranchia* sp., 5 cm; (G) *Pterygioteuthis* sp., 2 cm and (H) *Japatella diaphana*, 5 cm.

of squid using the relatively less damaging samplers of the ROV *Tiburón* from the *R/V Western Flyer* that could collect squid in nearly perfect condition.

After collection, squid were sacrificed by decapitation and severance of the commissure connecting the two optic lobes. Lenses were then dissected from the eyes by cutting a circle in the suspending muscle using iridectomy scissors.

Measurement of modulation transfer function

Immediately after dissection, lenses were placed in a hole in a thin metal or plastic plate with a diameter matching that of the lens. For this purpose, we removed the top, horizontal portion of the bit holders in a standard drill bit index. This provided a graded series of openings that nearly exactly matched the range of lens diameters we encountered in our study. For the lenses of *Dosidicus gigas*, which were larger than the largest bit size in the index, we used the top of a plastic rack designed to hold 50 ml centrifuge tubes. A small amount of suspending muscle left attached to the perimeter of the lens held the lens in place in the metal plate. The lens was

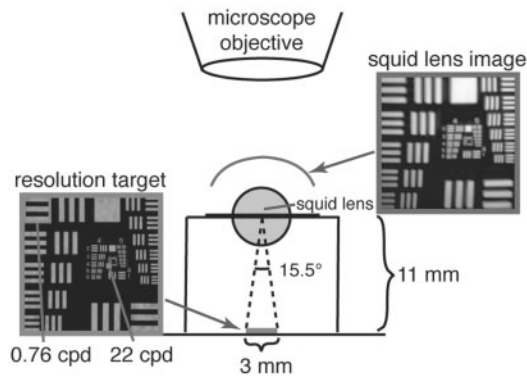


Fig. 2 Geometry of squid lens image measurement. Dissected squid lenses were mounted 11 mm above a 3 mm section of the resolution target. The diagram is drawn to scale, 'cpd' equals cycles per degree. The squid lens focused a curved image of the resolution target at an unknown distance above the squid lens. This image was then captured with a camera attached to a dissecting microscope.

then mounted 11 mm above a glass slide etched with the 1951 USAF resolution pattern (Edmund Optics, Barrington, NJ, USA) (Fig. 2). The lens and resolution target were placed on the stage of a Nikon SMZ-1500 dissecting microscope with a 1.6 \times or 0.5 \times Apochromat objective lens on a transilluminated brightfield base (Nikon). The power of the objective lens was chosen on the basis of the size of the squid lens being measured, with large lenses (>5 mm diameter) being measured with the 1.6 \times objective, and smaller lenses being measured with the 0.5 \times objective. A Nikon CoolPix 5000 digital camera was attached to the camera mount of the microscope. The image of the resolution target produced by the squid lens was focused in the digital camera using the camera's digital viewfinder. For maximal image quality, the f-stop of the camera was fixed to the highest allowed by the camera for the given light level, with a maximum of f8. Several color digital exposures (10–20) were taken with shutter speed bracketing underexposure and overexposure for a given lens setup. The camera was set to take color images at the highest possible resolution (2560 \times 1920 pixels) in JPEG format.

We used the dissecting microscope to photograph the resolution target without an intervening squid lens. The distance between the squid lens and the resolution target was smaller than the distance between the microscope objective and the resolution target, so the viewing angle subtended by the squid lens was larger than that of the microscope (Fig. 2). Because the spatial frequencies measured in the squid lens were well within the range where the MTF of the microscope itself is nearly 1, we ignored the

Table 1 Comparative modulation transfer functions

Species	Spatial frequency where 20% contrast remains, min. pupil (cycles per degree)
<i>Dryotriorchis spectabilis</i> (African serpent eagle)	70
<i>Homo sapiens</i> (human)	18 Vampyroteuthis <i>Japetella</i>
<i>Macaca nemestrina</i> (pig-tailed macaque)	16
<i>Gallus gallus</i> (domestic chicken)	9
<i>Oncorhynchus mykiss</i> (rainbow trout)	5 \leftarrow Decapod squid
<i>Felis catus</i> (house cat)	2 Vampyroteuthis <i>Japetella</i>
<i>Rana esculenta</i> (edible frog)	1.9
<i>Rattus norvegicus</i> (research rat)	1.1
<i>Phalanooides tristifica</i> (agaristid moth)	0.45
<i>Ocybadistes walkeri</i> (skipper butterfly)	0.32

Data from Krueger and Moser 1972; Bonds 1974; Robson and Enroth-Cugell 1978; Williams and Booth 1981; Land 1984; Artal and Navarro 1994; Jagger 1996; Artal et al. 1998; Coletta et al. 2003.

possible decrease, in contrast due to the optical path of the microscope and camera when calculating the modulation transfer function of the squid lens.

Using Photoshop (Adobe, San Jose, CA, USA), we cropped each squid image to the size of the 2nd series of pattern elements of the resolution target and rotated it so that the individual pattern elements made right angles to the edges of the image. Because of the geometry of our mounting setup, these elements were the ones in the pattern that could be imaged suitably well by the microscope. Given the geometry of the lens mount, the 2nd through 6th cycles of pattern elements of the target ranged from 0.76 to 22 cycles/degree, a range that brackets the resolution capabilities of most studied visual systems (Table 1). The brightness of these images was then adjusted using the "Auto Levels" command in Photoshop to ensure that the average brightness of each image we measured was comparable.

The cropped, rotated, and contrast-adjusted images were input into a custom-written MatLab program (MathWorks, Natick, MA, USA). To minimize the effect of chromatic aberration, this program separated the red, blue, and green channels of each image and allowed the user to specify the coordinates of a transect through each of the pattern elements of the resolution target. The red and blue images were discarded and the green image was chosen for analysis. For each image, coordinates of the uppermost part of each series of pattern elements were selected (Fig. 3, upper left panel). Then, the user specified the vertical coordinates of each individual pattern element within a series

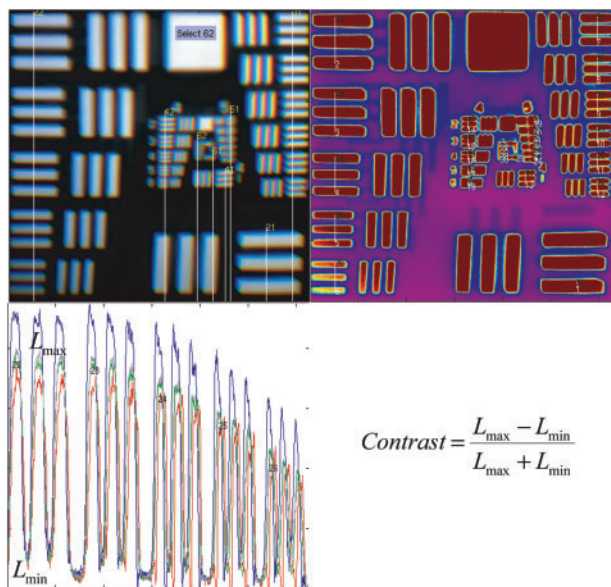


Fig. 3 Display of the program used to calculate MTF for each lens. Upper left panel shows the resolution target as imaged through a squid lens. The thin vertical lines indicate “slices” through the target to be analyzed for contrast in MATLAB. The lower left panel shows the contrast profile of a single “slice” through the resolution target. Notice that the overall difference between the maximum brightness level and the minimum brightness level decreases as the frequency of the pattern decreases. The red, green, and blue lines show the brightness levels of the red, green, and blue channels of the image, respectively. A reduction in peak-to-trough amplitude in the profile indicates a decrease in contrast. The upper right panel shows the final “slices” selected for each element of the resolution target as vertical white lines superimposed on the brightness values for a single channel of the original RGB image shown in a chromatic color scale. The lower right panel shows the expression used to calculate the modulation transfer of each pattern element in the resolution target.

of pattern elements (Fig. 3, upper right panel). The program then displayed the results of the coordinate selection (Fig. 3, lower left panel). The user could then adjust the coordinates of the location of each “slice” through a pattern element to correct for artifacts in the image such as slight lens scarring or uneven illumination. Finally, the program stored the designated coordinates as well as the maximum and minimum brightness values found within each designated transect of a pattern element.

A second MatLab program used these brightness values to calculate and plot the contrast for each frequency for each squid image, and fit an exponential curve to the data. We considered this exponential curve to be the best estimate of the modulation transfer function for each squid lens, since it approached zero with increasing spatial frequency although the data were somewhat noisy at high frequencies. The resulting MTF curves were generally

smooth and similar to results found using other methods of measuring the MTF of biological lenses such as retinal reflection (programs available upon request).

Results and discussion

Modulation transfer functions

Modulation transfer functions from both lenses of 55 individual squids from 12 mesopelagic species were calculated, resulting in a total of 96 lenses measured. Lenses from one *Bathyteuthis* sp., one *Planktiteuthis* sp., three *Vampyroteuthis infernalis*, three *Japetella diaphana*, four *Histioteuthis* sp., five *Galiteuthis* sp., five *Octopoteuthis* sp., five *Pterygioteuthis* sp., five *D. gigas*, six *Gonatus onyx*, seven *Chiroteuthis* sp., and 10 *Helicocranchia* sp. were measured for MTF. Of these, *D. gigas* was collected with line-and lure-techniques, *J. diaphana* and *Pterygioteuthis* were collected by trawling alone, *Planktiteuthis* sp., *Octopoteuthis* sp., and *Chiroteuthis* sp. were collected by ROV alone, and the others were collected using a combination of ROV and trawling techniques. Mantle lengths ranged from 1 cm in *Pterygioteuthis* to 75 cm in *D. gigas*, and lens diameters ranged from ~1 mm in *Pterygioteuthis* and to 40 mm in *D. gigas*.

Upon inspection, the majority of animals sampled had abraded lenses that destroyed most of the imaging capability of the lens. The oegopsid squid in this study have no corneas and usually no lidding mechanism with which to close the eye, so when introduced to a container, simple swimming abrades the fragile lens surface against the sides of the container. In the case of *D. gigas*, other squid often attacked hooked animals as they were pulled out of the water, and this seemed to be the source of much lens damage. It was impossible to obtain unabraded measurements for some species, notably *G. onyx*. We report data in this study from the eight species for which we were able to obtain MTF estimates from obviously unabraded lenses.

Our measurements of MTF are likely conservative because the experimental procedure involved sacrifice of the animal and subsequent dissection and mounting of an isolated lens in air. This procedure could only introduce damage to the lens with a corresponding decrease in the overall MTF. In addition, small fluctuations in the surface curvature of the lenses, which would have very little effect on image quality in seawater because of the close match between the refractive indices of water and the periphery of the lens, would have a greater effect in air. Therefore, we considered the MTF with the

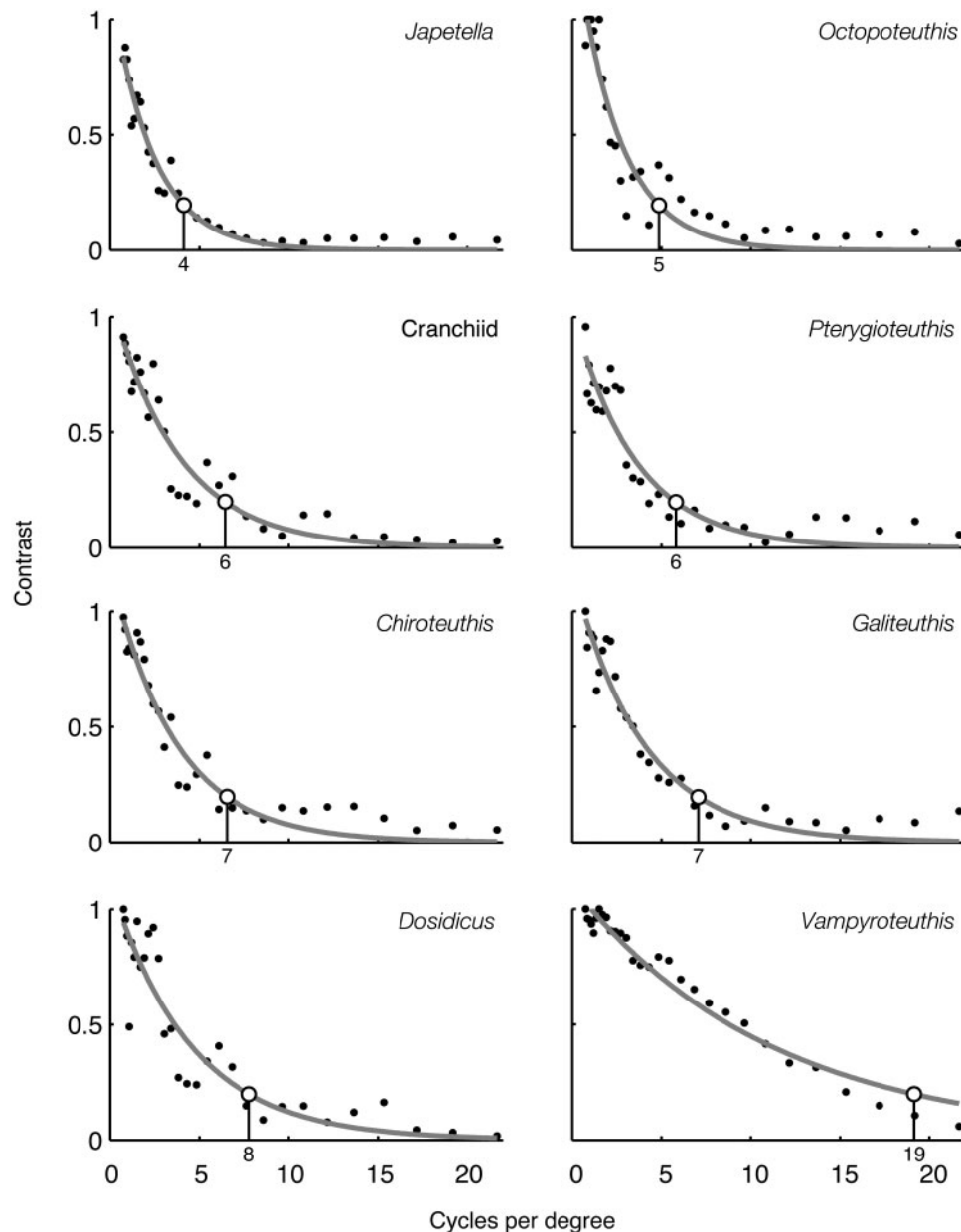


Fig. 4 Modulation transfer functions of mesopelagic cephalopods. Filled circles are contrasts measured directly from a given squid image. Grey lines are curves fitted to those points. Open circles indicate the intersection of the fitted curve with an arbitrary value of 20% remaining contrast.

highest resolution measured for each species to be the best representative of the MTF for the lens of a given species (Fig. 4).

The visual contrast threshold of an organism is the brightness contrast that can no longer be discriminated by the organism. In humans, this threshold is $\sim 1\%$. Measuring contrast threshold requires either behavioral experiments or electrophysiological recordings from the retina. Neither of these techniques is currently plausible for mesopelagic squid, and to our knowledge, a behavioral measurement of MTF has been attempted in only one coastal cephalopod species

(Mathger et al. 2006). Estimating the contrast threshold of these species is also problematic, since they view both extended objects illuminated by dim light and bioluminescent point sources. These tasks require different optical and retinal designs (Warrant and Locket 2004). The first task requires a sensitive retina with high levels of spatial and temporal summation and high contrast sensitivity. The second task requires no spatial or temporal summation in the retina, and contrast sensitivity is relatively unimportant. Therefore, we cannot *a priori* predict which frequencies in a lens are likely to be important in retinal

detection in any given species. The results of our lens acuity measurements, however, may indicate which type of vision a given squid possesses. We chose 20% contrast as a conservative cutoff value likely to be relevant to both types of visual systems in comparing the visual systems of squid to other squid and to more common terrestrial model species.

Interestingly, the one species of octopod measured in our data set, the pelagic *J. diaphana*, had the lowest MTF, which went below 20% contrast at 4 cycles/degree. The species with the highest visual capability in our data set was *V. infernalis*, reaching 20 cycles/degree before decreasing to 20% contrast (similar to that of humans) (Artal 1994). The mesopelagic decapod squid in our data set (several species of Cranchiid squid, *Pterygioteuthis* sp., *Chiroteuthis* sp., *Galiteuthis* sp., and *D. gigas*) had very comparable vision to one another and reached 20% contrast at frequencies ranging from 5 to 8 cycles/degree.

Table 1 compares the MTF of mesopelagic cephalopods with other taxa. We searched the literature for other optical (as opposed to behavioral) measurements of MTF in other species. The one species of octopod measured in our data set, *J. diaphana*, the species with the lowest resolving power has a lens comparable to that of the rainbow trout. The optical acuity of mesopelagic decapods falls between that of trout and macaques.

Metabolism and vision in the deep sea

Surprisingly, *Vampyroteuthis infernalis*, which is possibly the most basal cephalopod sampled here, has an optical acuity comparable to that of humans. Studies on metabolic rates have been an important means for understanding the organismal biology and ecology of pelagic species. For many groups of organisms, there is no correlation of depth and mass-specific metabolic rate. For fish and cephalopods, however, there is a negative correlation between depth and metabolism (Childress 1995). Several possible explanations for this correlation have been tested and rejected including: low oxygen concentrations at intermediate depths, lower food availability, lower temperatures, and increased hydrostatic pressure at depth.

The currently favored hypothesis is that with less ambient light available for predation, interactions happen at shorter distances and there has been a relaxation on selection for locomotory abilities in predators (Childress 1995). The data presented here are not especially consistent with this hypothesis. *Vampyroteuthis* and *Japetella* have the highest and lowest acuity vision measured here, and both have

extremely low metabolic rates (Seibel et al. 1997). The decapod squid, with highly variable metabolic rates, have very similar visual acuity. Thus, a simple metric such as visual interaction distance may not be sufficient to explain metabolic variation in cephalopods. We consider two other hypotheses to explain the patterns we observed in cephalopod visual capabilities.

While the number of taxa sampled here is admittedly small, evolutionary history is one hypothesis for explaining the patterns of optical acuity we measured. *Octopus* has a much lower diversity of S-crystallin sequence and charge than *Loligo opalescens*, the two taxa that have been comprehensively sampled for S-crystallin sequences (Sweeney et al. 2007). The one octopod in our study also had the lowest optical acuity. As described by Sweeney et al. (2007), diversity of S-crystallin charge and sequence may play a causative role in the evolution of lens quality in cephalopods. Preliminary SDS-PAGE experiments (A.M.S., unpublished) suggest that *Vampyroteuthis* lenses are also made almost completely of S-crystallins. Although the phylogenetic position of *Vampyroteuthis* is still uncertain, they may branch basal to octopod and decapod cephalopods (Lindgren et al. 2004; Strugnell et al. 2005). Major groups of fossil cephalopods, such as ammonites and belemnites, are not well enough preserved to know what their eye design might have been. The only extant cephalopod outgroup to the coleoids is *Nautilus*, which has a unique pinhole-chamber eye design. We hypothesize that the ancestor to coleoid cephalopods had a “*füllmasse*” eye design intermediate between a pinhole eye and an acute camera-like eye, as found in some gastropods and annelids (Land and Fernald 1992). Subsequent independent diversifications of S-crystallins in the three major coleoid lineages may then have led to the diversity of the optical capabilities we measured.

Another possibility is that the variation in cephalopod lens acuity relates to whether it is more important for a species to detect point sources of bioluminescence or reflected downwelling sunlight. For an eye to be sensitive to a scene illuminated by downwelling sunlight at depth, it must employ either spatial or temporal summation, or both (since the photon capture of any one photoreceptor will never be enough to produce a visual signal greater than the visual noise) and therefore selection pressure on optical acuity of the lens may be reduced. To detect point sources of bioluminescence, there are usually enough photons in any given bioluminescent display to be detected by a retina at distances of 10 to 100s of meters, and a very acute lens may be

required to locate this signal in space (Warrant and Lockett 2004). Another possibility is that in order to detect point sources at a distance on a retina with a very fine retinal mosaic, it is necessary to focus as many photons as possible onto a single photoreceptor, a task best accomplished with a very acute lens. Therefore, organisms primarily viewing bioluminescent displays will have increased selection pressure for very acute lenses. By examining lens acuity, we can generate hypotheses about predation and visual interactions in these organisms that are so exquisitely adapted for life in the deep sea.

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