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Two eyes for two purposes: *in situ* evidence for asymmetric vision in the cockeyed squids *Histioteuthis heteropsis* and *Stigmatoteuthis dofleini*

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The light environment of the mesopelagic realm of the ocean changes with both depth and viewer orientation, and this has probably driven the high diversity of visual adaptations found among its inhabitants. The mesopelagic 'cockeyed' squids of family Histioteuthidae have unusual eyes, as the left and right eyes are dimorphic in size, shape and sometimes lens pigmentation. This dimorphism may be an adaptation to the two different sources of light in the mesopelagic realm, with the large eye oriented upward to view objects silhouetted against the dim, downwelling sunlight and the small eye oriented slightly downward to view bioluminescent point sources. We used *in situ* video footage from remotely operated vehicles in the Monterey Submarine Canyon to observe the orientation behaviour of 152 *Histioteuthis heteropsis* and nine *Stigmatoteuthis dofleini*. We found evidence for upward orientation in the large eye and slightly downward orientation in the small eye, which was facilitated by a tail-up oblique body orientation. We also found that 65% of adult *H. heteropsis* ($n = 69$) had yellow pigmentation in the lens of the larger left eye, which may be used to break the counterillumination camouflage of their prey. Finally, we used visual modelling to show that the visual returns provided by increasing eye size are much higher for an upward-oriented eye than for a downward-oriented eye, which may explain the development of this unique visual strategy.

This article is part of the themed issue 'Vision in dim light'.

1. Introduction

The mesopelagic region of the deep sea (200–1000 m depth) is a dim to dark habitat, yet it contains the highest diversity of visual adaptations in the sea, indicating that vision remains important at these depths [1]. Two primary sources of light are available for mesopelagic vision: sunlight and bioluminescence. These light sources differ in both their spatial organizations and how they change in visual detectability with depth and viewer orientation [2]. This makes the relatively dark environment of the mesopelagic region a potentially fertile environment for eye evolution, as small changes in depth or viewer orientation may have large impacts on the visual scene encountered by an eye.

Dim, downwelling sunlight creates spatially extended scenes, where light reaches the eye from many different directions at once and the resulting image falls across multiple receptors. In dim light, these scenes are low in contrast and typically require high absolute sensitivity for detection. In comparison, bioluminescence typically functions as a high-contrast point source and thus calls for higher resolution in order to localize the emitted light [2]. As a result, while a larger eye will always be better for seeing either type of light, the optimal balance in trade-offs between sensitivity and resolution in an eye changes depending on which light source is being viewed [1].

The colour, intensity and spatial distribution of underwater light changes rapidly with depth. Downwelling sunlight attenuates exponentially, decreasing by roughly 1.5 orders of magnitude every 100 m in clear oceanic waters [3]. Additionally, absorption and scattering cause sunlight to become nearly monochromatic ($\lambda_{\text{max}} = 480 \text{ nm}$), more diffuse and more vertically symmetric with depth [4,5]. Like all emitted light, bioluminescence has highest contrast against a black background, so as downwelling sunlight decreases and limits the potential for viewing extended scenes, the contrast of bioluminescent emissions from mesopelagic organisms simultaneously increases [2].

The directionality of the mesopelagic light field makes viewer orientation another important factor in vision. Orientation determines not only the intensity of the background light reaching the eye, but also how the brightness of a visual target attenuates relative to the brightness of the background [6]. In particular, extended scenes produced by downwelling sunlight are easiest to detect when eyes are oriented directly upward. However, optimal detection of bioluminescence occurs where sunlight is minimized, so downward viewing angles increase the contrast of bioluminescent signals [2].

The change in visual scene that occurs with depth and viewer orientation and the contrasting impacts on the detection of extended scenes versus bioluminescence pose a major challenge to vision in the dim light of the mesopelagic realm. The histioteuthids are a family of mesopelagic squids that appear to have adapted to this challenge with a novel solution. Histioteuthids have dimorphic eyes, where the left eye can be more than twice the diameter of the right eye [7]. Upon hatching, paralarvae have small, bilaterally symmetrical eyes. However, the left eye enlarges during development of the juvenile to the extent that it pushes the head out of alignment with the mantle in some species [8]. While the smaller right eye maintains a typical hemispherical shape, the left eye becomes semi-tubular [8,9]. This dimorphism continues into the optic lobes, as the left lobe can be twice as large as the right [10,11]. Additionally, the lens in each histioteuthid eye can be differently pigmented, yielding divergent filtering effects on the light reaching each retina [9,11,12].

Early hypotheses predicted that the dimorphic histioteuthid eyes were adapted to the differing light levels in shallow versus deep water [9,13]. However, evidence that some histioteuthids exhibit diel vertical migration drew this into question, as occupying deeper water during the day and ascending shallower only at night would preclude bright light exposure [8,14]. An alternative hypothesis was based on angled ventral histioteuthid photophores thought to be used for counterillumination camouflage. In order to orient these photophores downward, histioteuthids were predicted to orient in a tail-up posture with the body axis at a 45° angle and the head twisted so that the large left eye orients upward to view objects silhouetted against the dim downwelling sunlight, while the smaller eye orients slightly downward to optimally detect flashes of bioluminescence [8]. This prediction has never been tested *in situ*, in part due to the inaccessibility of the deep-sea environment and the scarcity of live observations of midwater squids.

Histioteuthidae currently comprises 18 species: 15 in *Histioteuthis* and three in *Stigmatoteuthis* [15,16]. Our study targeted two species that partially overlap in both geographic and depth ranges: a large sample of *Histioteuthis heteropsis*, and a smaller sample of *Stigmatoteuthis dofleini* (figure 1).

We used over 25 years of *in situ* deep-sea video footage to determine (i) whether the large eye orients upward and the small eye downward, (ii) whether consistent postures and body orientations facilitate eye orientations and (iii) how lens pigmentation varies between eyes and individuals. We then used visual modelling to investigate the implications that the observed eye orientations and depths have for detection of extended scenes versus bioluminescent point sources in each eye.

2. Material and methods

(a) Study system

We used high-resolution *in situ* observations from the Monterey Submarine Canyon (Monterey Bay, CA, USA) from archived remotely operated vehicle (ROV) video footage at the Monterey Bay Aquarium Research Institute (MBARI). We analysed 152 encounters with *H. heteropsis* and nine encounters with *S. dofleini*, representing all histioteuthid sightings in MBARI's Video Annotation and Reference System from 1989 through July 2015 (figure 1) [17]. We categorized individuals as juveniles or adults based on morphological features such as transparency, relative arm length and fin dynamics (figure 2a) [7]. Owing to the vastness of the habitat and dynamic movement of water masses, it is unlikely that any observations were of the same individual, so we treat each encounter independently. For orientation measurements, we assumed that the top of the video frame was parallel with the ocean surface because MBARI ROVs are engineered to sit in a stable, horizontal position in the midwater. Finally, we assumed that observed postures and eye orientations were representative of natural behaviour, though the presence of the ROV and lights may disturb the animals.

(b) Eye orientations

We defined eye orientation as the absolute angle that the centre of the visual field deviated from an upward vertical position (figure 3a, left). In other words, an eye looking directly up would be oriented at 0° and an eye looking directly down would be at 180° . We determined the centre of the visual field by taking a still frame the first time we had a view perpendicular to the visual axis (a direct side view of the eye and lens), and then bisecting the two-dimensional image of the exposed lens. We measured eye orientation to the nearest 5° for each eye in each encounter when possible. This only occurred in a subset of video observations, and for some individuals we could only measure one eye.

(c) Posture and body orientation

We recorded initial body posture, which we divided into two categories: 'J-pose' (figure 2a) and 'Straight Arms' (figure 2b). In J-pose, the arms were curled up dorsally towards the head and mantle, as is seen in many other cephalopods [18–23]. In Straight Arms, the arms were extended and held together in line with the mantle, another posture also observed in some other deep-sea cephalopods [21,23,24]. Other postures were rarely observed (less than 1% on first approach).

We defined body axis as the absolute angle that the anterior–posterior mantle axis deviated from a tail-up vertical position (0°) (figure 3b). We measured body axis to the nearest 5° , and to avoid foreshortening we only made a measurement when the ROV camera had a directly lateral view of a squid (figure 3b). These measurements were always made at the earliest opportunity after spotting a squid with the ROV to minimize disturbance effects. We performed all orientation statistics in R v. 3.1.1 using *circular* [25,26].

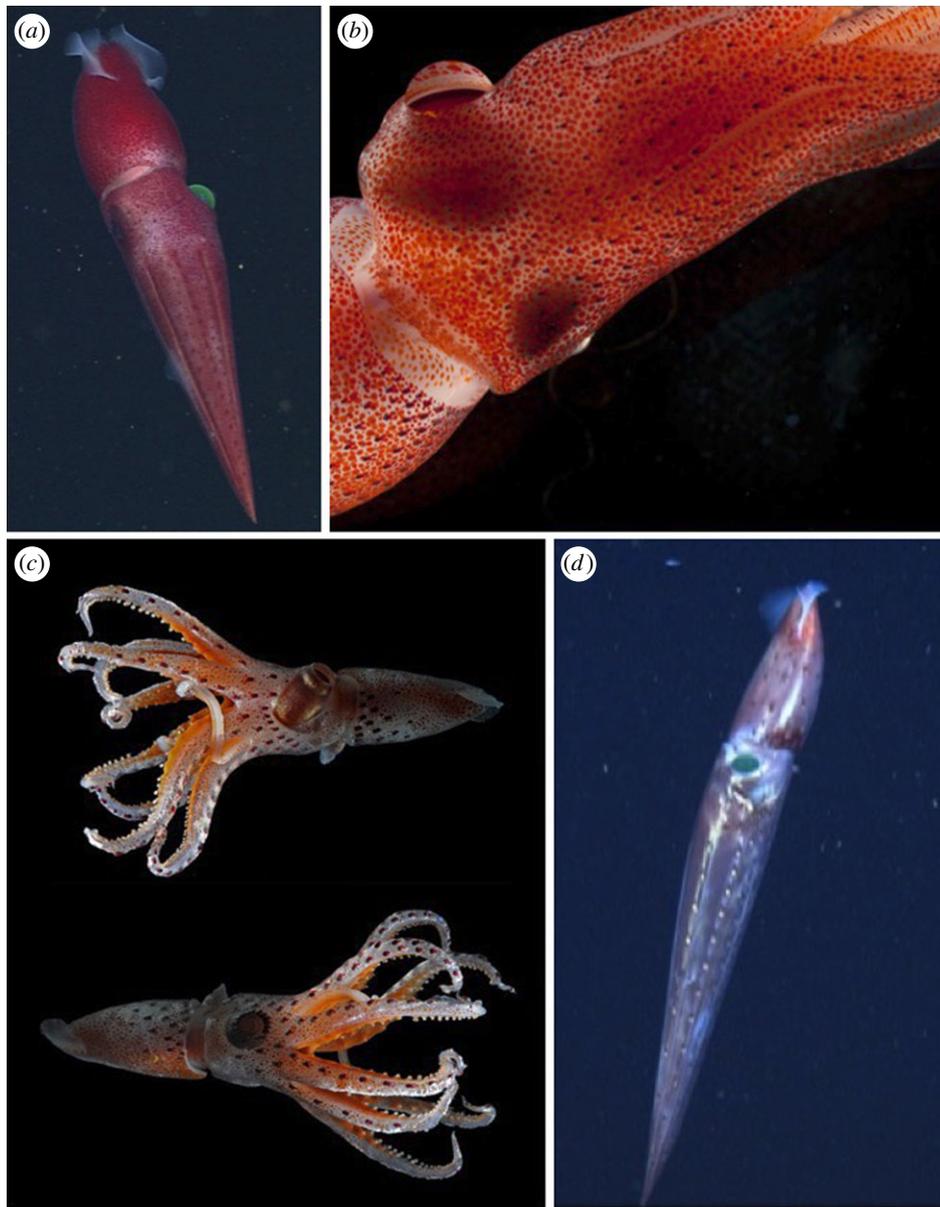


Figure 1. The two species examined in this study: (a) an adult *Histiototeuthis heteropsis* (ROV image), (b) a semi-transparent juvenile *H. heteropsis* showing the differently sized and shaped eyes, (c) the left and right side of a juvenile *Stigmatoteuthis dofleini*, and (d) an adult *S. dofleini* (ROV image).

(d) Lens filtering

Yellow pigmentation in the large left eye of some individuals was evident in the ROV footage (figure 2c; electronic supplementary material, video S1), so we classified each lens of each eye as pigmented or unpigmented. Additionally, we captured three *H. heteropsis* and one *S. dofleini* after filming with the ROV and brought them aboard the ship, where we confirmed our classifications of lens pigmentation in all specimens by direct observation and via lens transmittance measurements. We measured the spectral transmittance of each large and small lens based on published methods [27]. An OceanOptics LS-1 light source was mounted directly above the lens and collimated to make a 4 mm diameter beam for diffuse lighting. Freshly dissected lenses were placed on a Gershun tube mounted to an OceanOptics USB2000 spectrometer and relative transmittance through the lens was measured from 350 to 800 nm using SpectraSuite software. We defined the cut-off wavelength for filtering as $T_{0.5}$, the wavelength at which the transmittance was halfway between the maximum and minimum transmittance.

(e) Depth

We extracted the depths recorded at first sight of each individual using CTD data from the ROVs (figure 4). We assigned

depth observations to 50 m bins and then adjusted counts for differences in total ROV sampling time across each depth bin.

(f) Visual modelling

We modelled the change in sighting distance as a function of eye size and viewer orientation for point-source bioluminescence (emittance of 10^{10} photons s^{-1}) and a 1 cm wide black object (a realistic prey size) using a published computational model of mesopelagic vision [28]. This model takes a statistical approach to visual detection, in which an eye must reliably distinguish the number of photons from the target versus the number of photons from the background. The model also assumes optimal spatial summation so that the 'pixel' of the eye is the same width as the target to give an upper limit on sighting distance. Model parameters for vision included an integration time of 0.16 s, lens ratio of 2.55, retinal quantum efficiency of 0.36, dark noise of $2.80 \times 10^{-5} s^{-1}$ and rhabdom diameter of $4 \mu m$ [28]. We modelled the light field from maximum surface irradiance (midday sun) and selected three depths (300, 400 and 500 m) within the histiototeuthid depth range that demonstrated changes in visual performance with light attenuation [28]. We also assumed clear oceanic water (Jerlov Type 1) [5]. Our model is, therefore, a best-case scenario

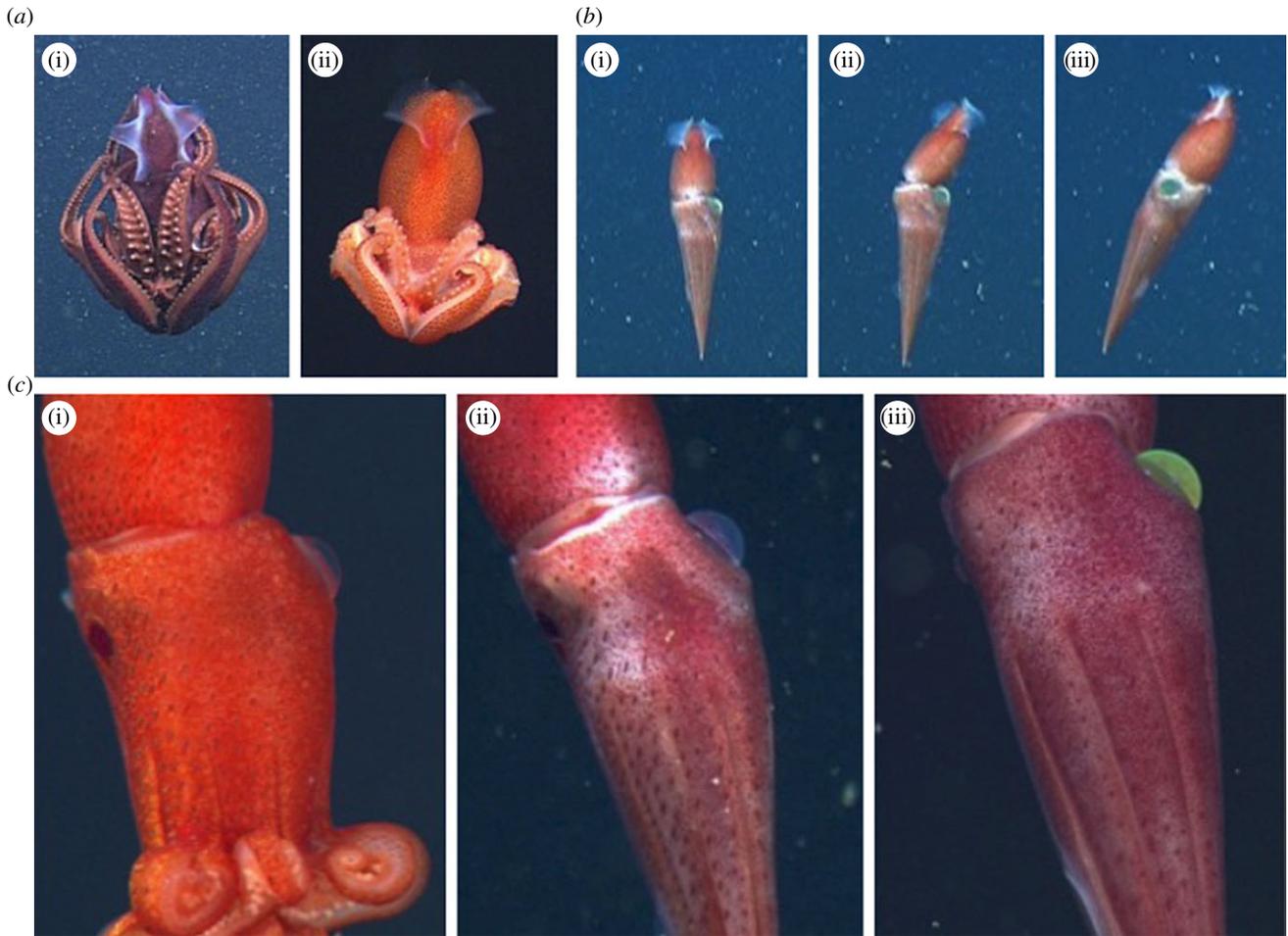


Figure 2. Still frames of *Histioteuthis heteropsis* from *in situ* ROV video. (a) Examples of an adult (i) and a juvenile (ii) in the J-pose posture. (b) Sequential images (i–iii) of a ‘ratcheting’ turn in the Straight Arms posture. The sequence shows the starting position (i), twisting of the mantle relative to the head (ii), and the ending position (iii). (c) A juvenile (i) and adult (ii) with unpigmented large left lenses, and an adult (iii) with a yellow-pigmented left lens.

for visual detection given optical parameters, and the values for sighting ranges are probably significant overestimates. However, the important relationships between sighting distances, pupil size, depth, viewer orientation and visual target type, which are the main focus of our analyses, are robust.

3. Results

(a) Eye orientations

In both species studied, the large left eye had an upward orientation and the smaller eye a slightly downward orientation (figure 3a). Adult *H. heteropsis* oriented the large left eye between horizontal and upward at $45 \pm 14^\circ$ (mean \pm s.d.), and orientations were not uniformly distributed in space (Rao spacing test, $n = 29$, $U = 298$, $p < 0.001$). The small right eye was oriented between horizontal and downward at $123 \pm 13^\circ$ and orientations were not uniformly distributed in space (Rao spacing test, $n = 23$, $U = 294$, $p < 0.001$). While most juveniles were in J-pose with their arms covering their eyes, those that could be measured oriented their left eye upward at $48 \pm 3^\circ$ ($n = 3$) and their right eye slightly downward at $125 \pm 7^\circ$ ($n = 2$). *Stigmatoteuthis dofleini* exhibited similar eye orientations, with the left eye upward at $35 \pm 12^\circ$ and not uniformly distributed (Rao spacing test, $n = 5$, $U = 258$, $p < 0.001$) and the right eye slightly downward at $122^\circ \pm 4^\circ$ and not uniformly distributed (Rao spacing test, $n = 5$, $U = 278$, $p < 0.001$). Mean eye orientations for adult

H. heteropsis, juvenile *H. heteropsis* and *S. dofleini* (figure 3a) were not significantly different for the large left eye (Watson–Williams test, $F = 1.43$, d.f.₁ = 2, d.f.₂ = 34, $p = 0.2553$) or the small right eye (Watson–Williams test, $F = 0.068$, d.f.₁ = 2, d.f.₂ = 27, $p = 0.89$).

A published cross section through both eyes of *S. dofleini* shows that the large, semi-tubular left eye has an approximately 90° field of view, while the small, hemispherical right eye has a larger field of view of approximately 155° (figure 3c) [8]. With the visual axis oriented at 45° , the large eye receives light from the area directly above (0°) to horizontal (90°) on the left side. With the visual axis oriented at 120° , the small eye receives light from 43° to 198° and fully views light coming from both below and horizontally on the right side (figure 3c).

When an individual was measured multiple times its eye orientation angles tended to be consistent, and eye movements relative to the head were not observed over short timescales throughout the video observations. We, however, observed one specimen each of *H. heteropsis* and *S. dofleini* trapped upside down (head up) in ROV collection containers, and the large eye in each was rotated anteriorly, demonstrating that movement is possible (electronic supplementary material, figure S1). We did not observe any indication of eye movement in the small eye of any individual. Adults of both species commonly engaged in a turning behaviour seen once previously and termed ‘ratcheting,’ in which the mantle turned relative to the head and then the head snapped around to rejoin it (figure 2b; electronic supplementary

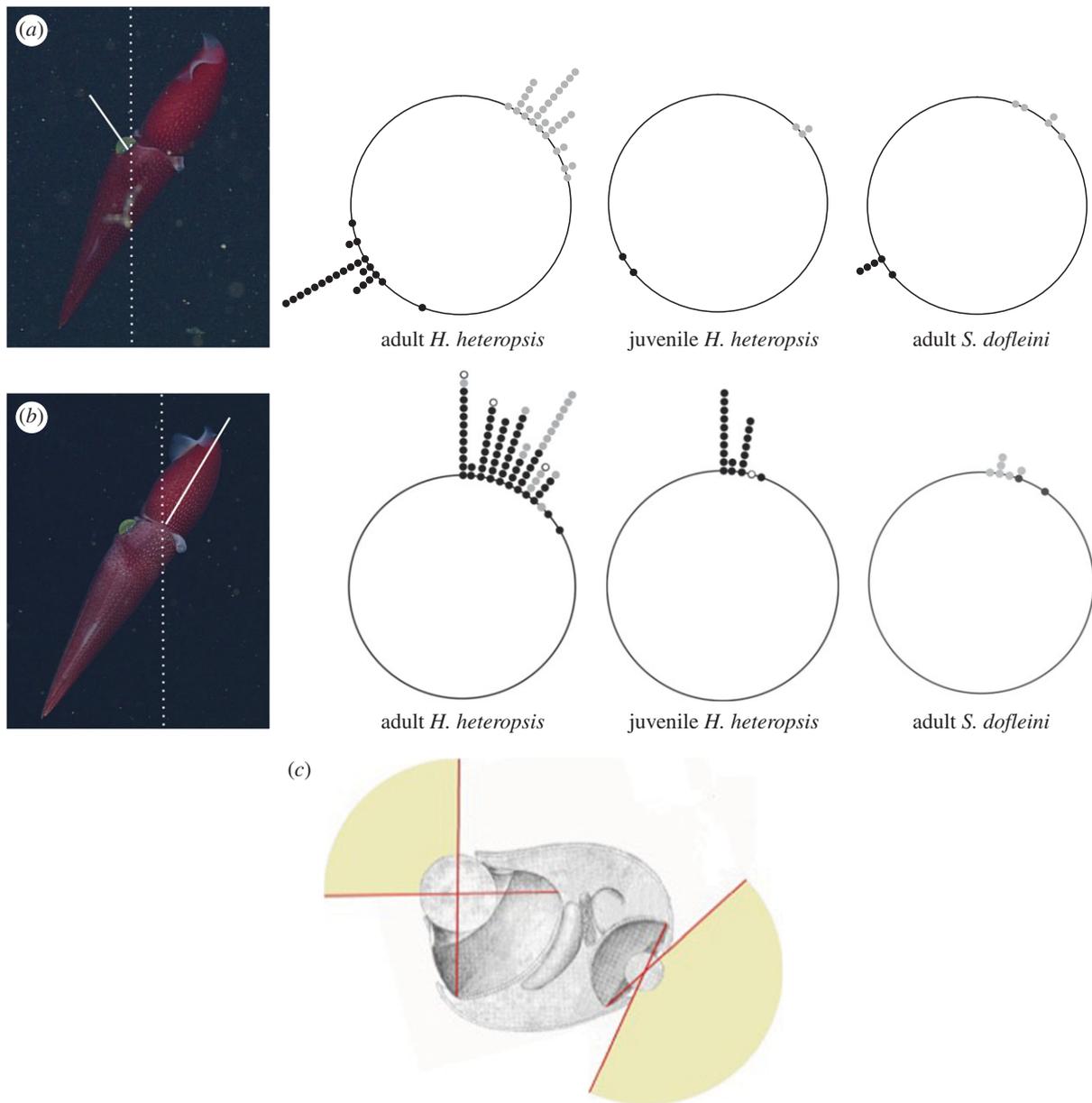


Figure 3. Histioteuthid eye and body axis orientations (left, solid white lines) relative to a vertical axis (left, dotted white lines). (a) Absolute eye orientations, with 0° indicating an eye oriented directly upward and 180° directly downward. Orientations of the larger, left eye are plotted on the right (grey) and the smaller, right eye on the left (black) to show where the eyes are directed relative to one another. (b) Absolute body axis orientations with 0° indicating a vertical, tail-up position and 180° representing a vertical, tail-down position. Observations are shaded by posture observed at first sight of the animal: J-pose (black), Straight Arms (grey), or unknown/unseen (unfilled). (c) A cross section through both eyes of a histioteuthid showing the approximate field of view for each eye (shaded) given an orientation of 45° for the large left eye and 120° for the small right eye. Adapted with permission from Young [8]. (Online version in colour.)

material, videos S2 and S3) [29]. Eye orientations were maintained relative to the surface during these turns.

(b) Posture and body orientation

All histioteuthids observed ($n = 161$) oriented the head and arms downward with the posterior mantle upward in a vertical or oblique position throughout all observations. Squid were primarily found in a J-pose or Straight Arms posture (figure 3), and if they changed posture during an observation period they alternated between these two poses. *Histioteuthis heteropsis* adult body axes were oblique to vertical at $20 \pm 14^\circ$ ($n = 76$), while juveniles had more vertical body axes at $5 \pm 6^\circ$ ($n = 21$) (figure 3b). *Stigmatoteuthis dofleini* had oblique to vertical body axes at $16 \pm 9^\circ$ ($n = 8$). The mean body axis of *H. heteropsis* encountered in the J-pose posture ($18 \pm 14^\circ$,

$n = 56$) was significantly more vertical (Watson–Williams test, $F = 11.2$, $d.f._1 = 1$, $d.f._2 = 71$, $p = 0.001$) than that of squid encountered in the straight-arm posture ($29 \pm 10^\circ$, $n = 17$) (figure 3b).

(c) Lens filtering

The lens from the larger left eye varied in pigmentation between individuals. From video analysis, the left lenses in all juvenile *H. heteropsis* ($n = 18$) were unpigmented, while the left lenses in 35% of adults were unpigmented ($n = 24$) but were yellow-pigmented in the remainder ($n = 45$) (figure 2c). All *S. dofleini* observed ($n = 7$) were adults with pigmented left lenses. We measured lens transmittance in both eyes of three *H. heteropsis* with unpigmented left lenses and one *S. dofleini* with a pigmented left lens. The *H. heteropsis* lenses that appeared unpigmented

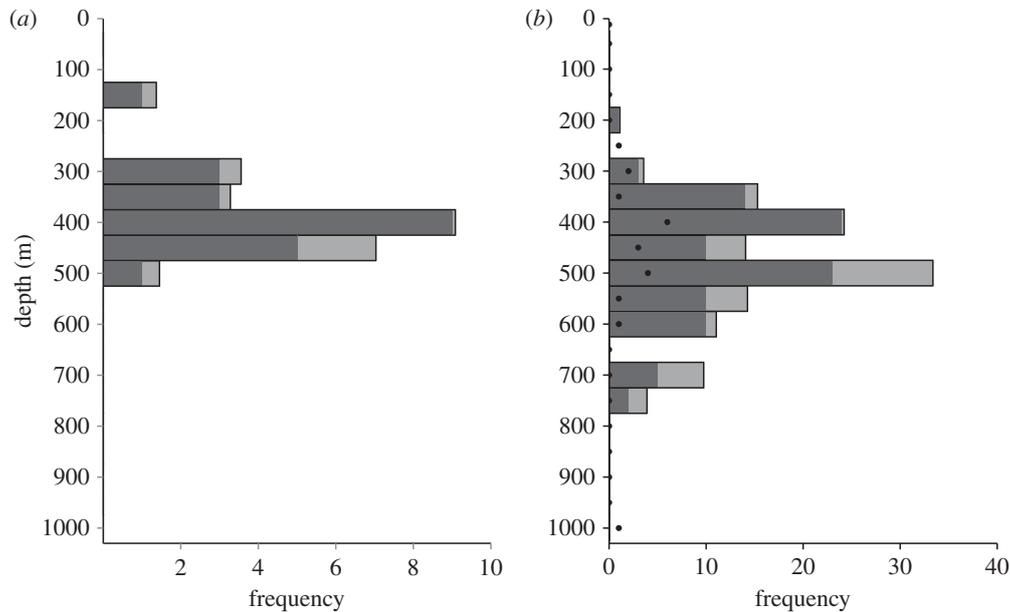


Figure 4. Depth distributions of *H. heteropsis* for (a) juveniles and (b) adults. Darker portions of bars indicate true counts of individuals, while lighter portions correct for total ROV effort in each depth bin over the period studied. Black points indicate the true counts of *H. heteropsis* that could not be identified to life stage. Juveniles occurred significantly shallower than adults (Welch Two Sample *t*-test, $p < 0.0001$).

also showed no evidence of spectral filtering, while the yellow-pigmented lens of *S. dofleini* acted as a cut-off filter with 50% transmittance at 465 nm. As in a previous report [12], the transmittance spectrum of a lens was unaffected by freezing and thawing. The small right lens appeared unpigmented across all specimens of both species and showed no evidence of spectral filtering.

(d) Depth

Juvenile *H. heteropsis* occurred at depths of 173 to 487 m (mean = 390 m, s.d. = 72, $n = 22$) (figure 4a), while adults were found significantly deeper (Welch Two Sample *t*-test, $t = -4.40$, d.f. = 44.8, $p < 0.0001$) from 200 to 766 m (mean = 472 m, s.d. = 109, $n = 102$) (figure 4b). Some *H. heteropsis* individuals ($n = 20$) were not filmed closely enough to be identified to life stage (figure 4b). *Histioteuthis heteropsis* depth reports are primarily daytime sightings (07.00 to 19.00 PST), but four individuals were seen at other times (mean = 542 m, s.d. = 109). Adult *S. dofleini* occurred from 325 to 521 m (mean = 405, s.d. = 78.4, $n = 9$). *Histioteuthis heteropsis* with yellow-pigmented ($n = 42$) versus unpigmented ($n = 42$) left lenses had significantly different mean depths (Welch Two Sample *t*-test, $n = 84$, $t = -2.60$, d.f. = 77.1, $p = 0.011$), but this did not hold when juveniles were excluded from analysis (Welch Two Sample *t*-test, $t = -1.00$, d.f. = 34.9, $p = 0.323$).

(e) Visual modelling

Visual modelling demonstrated that while a larger eye performs better at detecting both a black object and a point-source of bioluminescence in any given orientation, the gains in sighting distances with increased pupil diameter are most pronounced for an eye oriented directly upward and viewing a black target illuminated by downwelling sunlight (figure 5). Viewing a black target gets dramatically more difficult with depth, approximately a 10-fold decrease in sighting distance for every 100 m increase in depth. Conversely, viewing point sources becomes slightly easier with depth in the depth range modelled, as the background light decreases.

A captured specimen of *S. dofleini* with a 65 mm mantle length had an 11 mm diameter yellow lens in the large eye and a 6 mm diameter unpigmented lens in the small eye. Both a small (e.g. 6 mm aperture), horizontal- or downward-oriented and a large (e.g. 11 mm aperture), upward-oriented histioteuthid eye perform well at viewing a bioluminescent point source. However, the smaller, horizontal- or downward-oriented eye performs very poorly at viewing a black target, partially because of its reduced aperture but primarily due to its viewing angle, and thus much darker background radiance. For example, at a depth of 300 m, for a downward-looking eye to see a black object at the same distance as a 1.5 mm diameter pupil that was looking up, it would need a pupil diameter of 40 mm.

4. Discussion

Our *in situ* observations of eye orientation, body posture and behaviour in *H. heteropsis* and *S. dofleini* provide evidence that the enlarged left eye looks upward and the smaller right eye slightly downward (figure 3a,c) [8]. The behavioural consistency of observed eye orientations across two species leads us to conclude that the dimorphic eyes of histioteuthids are a response to the highly directional light field of the mesopelagic zone [8], rather than an adaptation to differing brightness in shallow versus deeper water [9,13,30]. It should be noted that some mesopelagic fish have addressed the same challenge by developing 'secondary eyes' or 'accessory eyes' for looking downward, derived from their principal, upward-looking eyes [31–33]. Histioteuthid body orientations, depth distributions, dimorphic lens pigmentation and visual modelling support the conclusion that the larger left histioteuthid eye is adapted for upward-viewing.

However, the large left eye did not orient directly upward, but at a mean angle of 45° in adult *H. heteropsis* and 50° in *S. dofleini* (figure 3a). The small eye oriented slightly downward, around 120°, in both species. Despite a clear ability to move the left eye (electronic supplementary

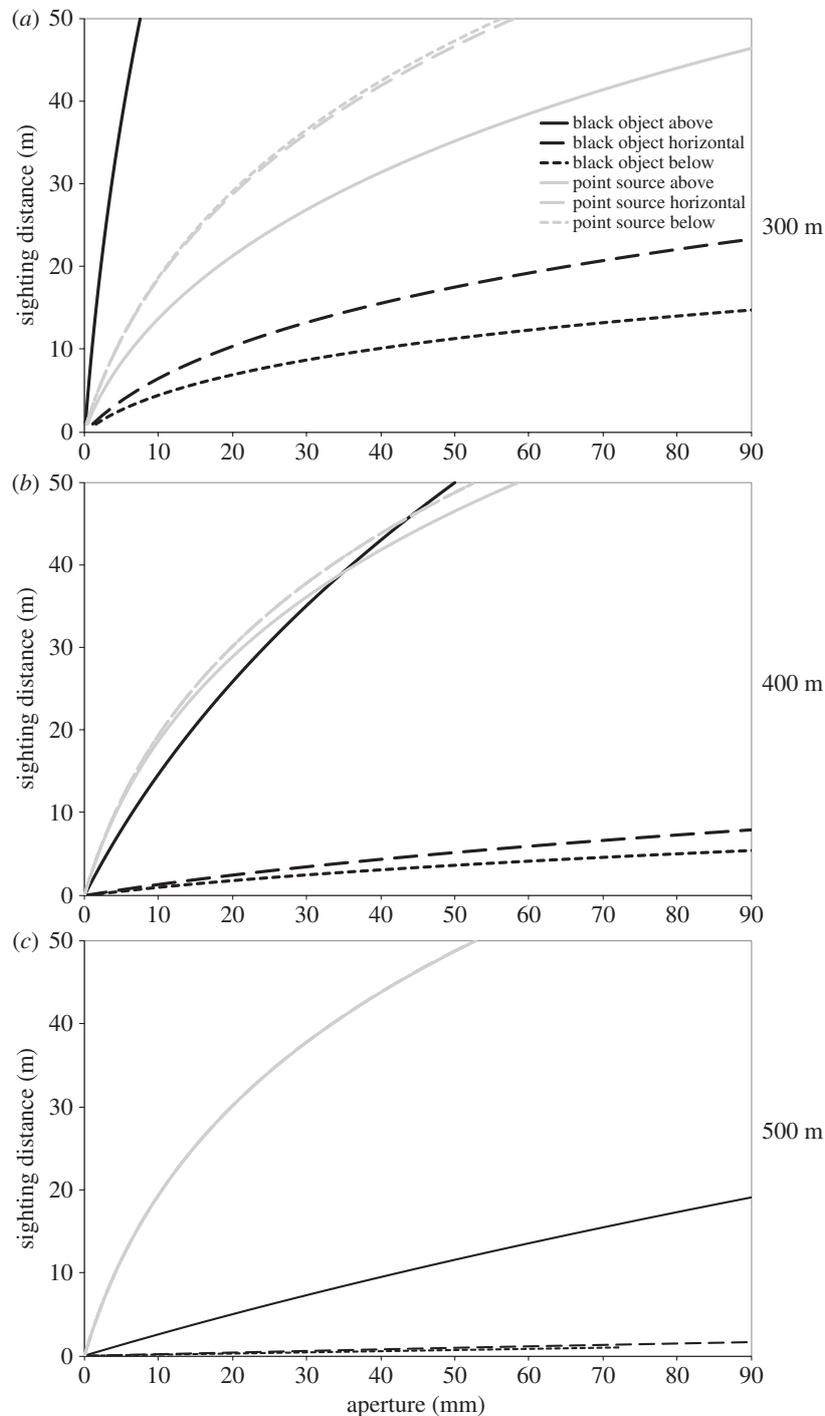


Figure 5. Theoretical maximum sighting distances for a 1 cm wide black object versus a point source of bioluminescence with changing aperture size and viewing angle at (a) 300 m, (b) 400 m and (c) 500 m.

material, figure S1) here and in previous records [8], we did not observe any eye movement in free-swimming squid and saw consistent eye orientations across two histioteuthid species (figure 3a). Additionally, we observed a common turning behaviour unique to histioteuthid squids that maintains eye orientations on a vertical axis during turns. In this turning behaviour, seen once previously in a histioteuthid and termed 'ratcheting' [29], the mantle turns relative to the head and then the head snaps around to rejoin the mantle (figure 2b; electronic supplementary material, videos S2 and S3). Squid appeared to have fine muscular control over the extent of the turn and the precise stopping point. This may allow histioteuthids to compensate for the unbalanced fields of view created by dimorphic eyes (figure 3c) and rapidly change which direction each eye is facing, or to scan their environment

during a slower turn while keeping the larger eye oriented upward and the smaller eye slightly down.

There is a risk, as with any ROV behavioural study, that the presence of the vehicle altered the natural behaviour of the animals [18], and it is possible that eyes were directed horizontally towards the ROV more than they would be in undisturbed squid. However, these squid may maintain a horizontal component to vision in their large eye in order to balance their fields of view around the body. Histological evidence supports this, as rhabdom length, retinal thickness and receptor packing vary across the retinas of both eyes and may be regionally specialized towards the horizontal and vertical axes of the fields of view [8,11]. The field of view for the large left eye included the region directly overhead to horizontal (figure 3c). The semi-tubular shape of

the eye should increase sensitivity but also restricts the field of view to about 90°, a beneficial trade-off for an eye that primarily views dim, downwelling sunlight [8]. The smaller right eye has a broad field of view similar to that of a human eye, and encompassed an area from directly below to well-above horizontal. This orientation would work well for an eye monitoring a large volume of dark water for bioluminescent flashes [8].

Eye orientations were produced via two characteristic body postures found in both histioteuthids, and individuals frequently moved between the two postures during an observation. In the position we termed ‘Straight Arms’ (figure 1*a,d*), the mantle was generally oriented at an oblique angle with the head down, as predicted [8]. This orients the angled ventral photophores downward so that they may be used for counterillumination camouflage [8,34]. The other posture was ‘J-pose’, in which the arms were wrapped dorsally towards the head and mantle (figure 2*a*). This pose is common among cephalopods and may be a defensive pose [18,35]; we noted *H. heteropsis* in this posture in the presence of potential predators (e.g. *Dosidicus gigas*) and after physical contact with the ROV. In J-pose the mantle orientations were closer to vertical (figure 3*b*), where counterillumination would not be as effective. Thus, the high incidence of J-pose in our observations may be a result of disturbance by the ROV, and Straight Arms may be a more undisturbed posture in these squids.

We saw variation in lens pigmentation in the large left eye of *H. heteropsis*, with more than half of adults displaying yellow pigmentation in the lens (figure 2*c*). This probably occurs with age and development, as juveniles did not show evidence of lens pigmentation. Additionally, we saw yellow pigment in the large left lenses of adult *S. dofleini*, while no lens pigmentation is reported in small specimens [12]. Previous records of lens pigmentation in histioteuthids are variable across species and are based on few specimens, but the large lens is consistently more heavily pigmented than the small lens and the pigment is most concentrated in the outer layers of the large lens [9,11,12].

Yellow lenses are common in upward-looking deep-sea fish and are thought to help break counterillumination camouflage by enhancing spectral differences between downwelling sunlight and bioluminescent camouflage [12,36]. We found that the pigmented left lens in *S. dofleini* acted as a high-pass cut-off filter with 50% transmittance at approximately 465 nm, close to the dominant wavelength of downwelling sunlight and similar to pigment absorbance previously reported via different methods [12]. Thus, the development of yellow filters in the upward-facing large histioteuthid lens may coincide with a shift in diet towards counterilluminating prey. Indeed, adult histioteuthids are known to eat counterilluminating organisms such as shrimp, myctophid lanternfishes, and other cephalopods, while juveniles primarily eat copepods and euphausiids [7,15,37,38].

Our ROV sampling of *H. heteropsis* depth distributions in the Monterey Canyon closely matched daytime depths

previously reported through trawling off southern California [14]. Histioteuthids were rarely seen deeper than 800 m, which approaches the lower limit for the detection of downwelling sunlight [39]. We found additional evidence of ontogenetic descent in *H. heteropsis*, with juveniles occupying shallower depths than adults (figure 4). This is consistent with patterns seen in other histioteuthid species [8,37] and indicates that the dimorphic enlargement of the left histioteuthid eye that occurs throughout development is concurrent with a descent into deeper, dimmer waters of the mesopelagic region.

Visual modelling indicated that the observed orientations of the large and small eyes of histioteuthids were probably important to the evolution of the size dimorphism. When looking at extended scenes, it is nearly impossible to recover the sighting range that is lost going from an upward- to a downward-oriented eye of any size (figure 5). However, sighting ranges for point-source bioluminescence do not change as substantially with viewing angle. Thus, for an upward-oriented eye viewing a black object, small increases in lens diameter (aperture) produce large gains in sighting distances. However, for a downward-oriented eye viewing a black object, even large increases in lens diameter do little to improve sighting distances. Eyes are metabolically expensive to grow, maintain, and use, so while larger eyes can improve both sensitivity and resolution, selection probably favours an eye just large enough to perform a necessary visual task but no larger [40]. Thus, once each eye has been consistently designated as upward-viewing or horizontal- to downward-viewing through behaviour, it is not difficult to imagine how selection could have favoured increasingly dimorphic specializations in each eye of the ‘cockeyed’ squids.

Data accessibility. Original ROV video is archived at the Monterey Bay Aquarium Research Institute (Moss Landing, CA, USA).

Authors’ contributions. K.N.T., B.H.R. and S.J. designed the study, K.N.T. and B.H.R. collected and analysed the data, K.N.T. and S.J. performed visual modelling, K.N.T. drafted the manuscript and all authors contributed to the writing and gave final approval for publication.

Competing interests. S.J. has had previous collaborations and co-authorships with the guest editor of this issue.

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