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Losing focus: how lens position and viewing angle affect the function of multifocal lenses in fishes

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Light rays of different wavelengths are focused at different distances when they pass through a lens (longitudinal chromatic aberration [LCA]). For animals with color vision this can pose a serious problem, because in order to perceive a sharp image the rays must be focused at the shallow plane of the photoreceptor's outer segments in the retina. A variety of fish and tetrapods have been found to possess multifocal lenses, which correct for LCA by assigning concentric zones to correctly focus specific wavelengths. Each zone receives light from a specific beam entrance position (BEP) (the lateral distance between incoming light and the center of the lens). Any occlusion of incoming light at specific BEPs changes the composition of the wavelengths that are correctly focused on the retina. Here, we calculated the effect of lens position relative to the plane of the iris and light entering the eye at oblique angles on how much of the lens was involved in focusing the image on the retina (measured as the availability of BEPs). We used rotational photography of fish eyes and mathematical modeling to quantify the degree of lens occlusion. We found that, at most lens positions and viewing angles, there was a decrease of BEP availability and in some cases complete absence of some BEPs. Given the implications of these effects on image quality, we postulate that three morphological features (aphakic spaces, curvature of the iris, and intraretinal variability in spectral sensitivity) may, in part, be adaptations to mitigate the loss of spectral image quality in the periphery of the eyes of fishes.

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1. INTRODUCTION

Vision is an important source of information for many animals. It provides nearly instantaneous information about the location, orientation, shape, motion, size, color, and polarization properties of objects both near and far [1]. In camera-type eyes such as those of vertebrates, light is transmitted through a highly refractive optical system (cornea and lens) and is then projected onto a sensor array (retina) at the back of the eye. Because the degree of focusing power of a lens is governed by its refractive index relative to its surroundings (air or water outside and aqueous humor inside the eye) and refraction is wavelength specific (due to dispersion), different wavelengths are focused at different distances from the center of the lens, an effect known as longitudinal chromatic aberration (LCA). This effect presents an optical challenge because the maintenance of a clear sharp image depends on the light coming to a sharp focus at the appropriate plane in the retina. For most animals, this presents a problem because many are sensitive to a broad spectrum of wavelengths: birds and fishes are often sensitive to wavelengths as low as 300–350 nm [2,3] while many fishes, amphibians, and reptiles can be sensitive to wavelengths over 700 nm [4–6]. To date, three different solutions to the problem of LCA have been found in nature. One is to have larger, and therefore physiologically more costly, eyes with a large f-number [1]. This solution results in a large depth of focus where LCA is negligible. A second solution is to position photoreceptors sensitive to different wavelengths at different distances from the lens, with shorter-wavelength-sensitive receptors positioned closer to the lens and longer-wavelength-sensitive receptors positioned farther away. Such banked retinas are known in firefly squid (*Watasenia scintillans*) [7], jumping spiders (*Plexippus validus*) [8], and deep-sea fish [9] where they are thought to minimize LCA (among other functions). A third solution is to possess a lens that corrects for LCA. Such lenses are known as multifocal lenses and have been found in a variety of fishes [10–15] and tetrapods [16–19].

Multifocal lenses function by correctly focusing only on the wavelengths that the retina maximally absorbs [10,20]. This is achieved by assigning parts of the lens to focusing certain wavelengths (Fig. 1). The effect can be observed by transmitting a monochromatic beam through the lens at different positions. The lateral distance between an incoming beam of light and the lens' optical axis is called the beam entrance position (BEP). For multifocal lenses, each BEP has a different focal length for monochromatic light. Because of dispersion, different BEPs have the same focal length for different wavelengths. Only one wavelength comes to focus at each BEP, and any other wavelengths get defocused at that specific BEP. Because there is a limited number of BEPs in one lens (the lens radius is finite), assigning a wavelength to a BEP prevents that BEP from focusing any other wavelength at the plane of the retina. Ideally, the lens focuses the wavelengths that the retina is most sensitive to and defocuses wavelengths that the retina is least sensitive to—in this situation, the lens and retina are said to be matched [10,20]. Because the retina is least sensitive to the defocused wavelengths and maximally sensitive to the focused ones, the total sum of these focused and defocused wavelengths results in a superior image {see Fig. 1(a) and [20] for a quantitative analysis of this improvement}.

The interaction between the correction for LCA at specific wavelengths by the presence of a multifocal lens and the spectral sensitivity of the retina implies that selective pressures that drive the spectral tuning of the retina also must affect the multifocal lens. Given the diversity of spectral environments in the aquatic world [21], such effects will be most apparent in fishes. There is a wealth of evidence supporting the hypothesis that

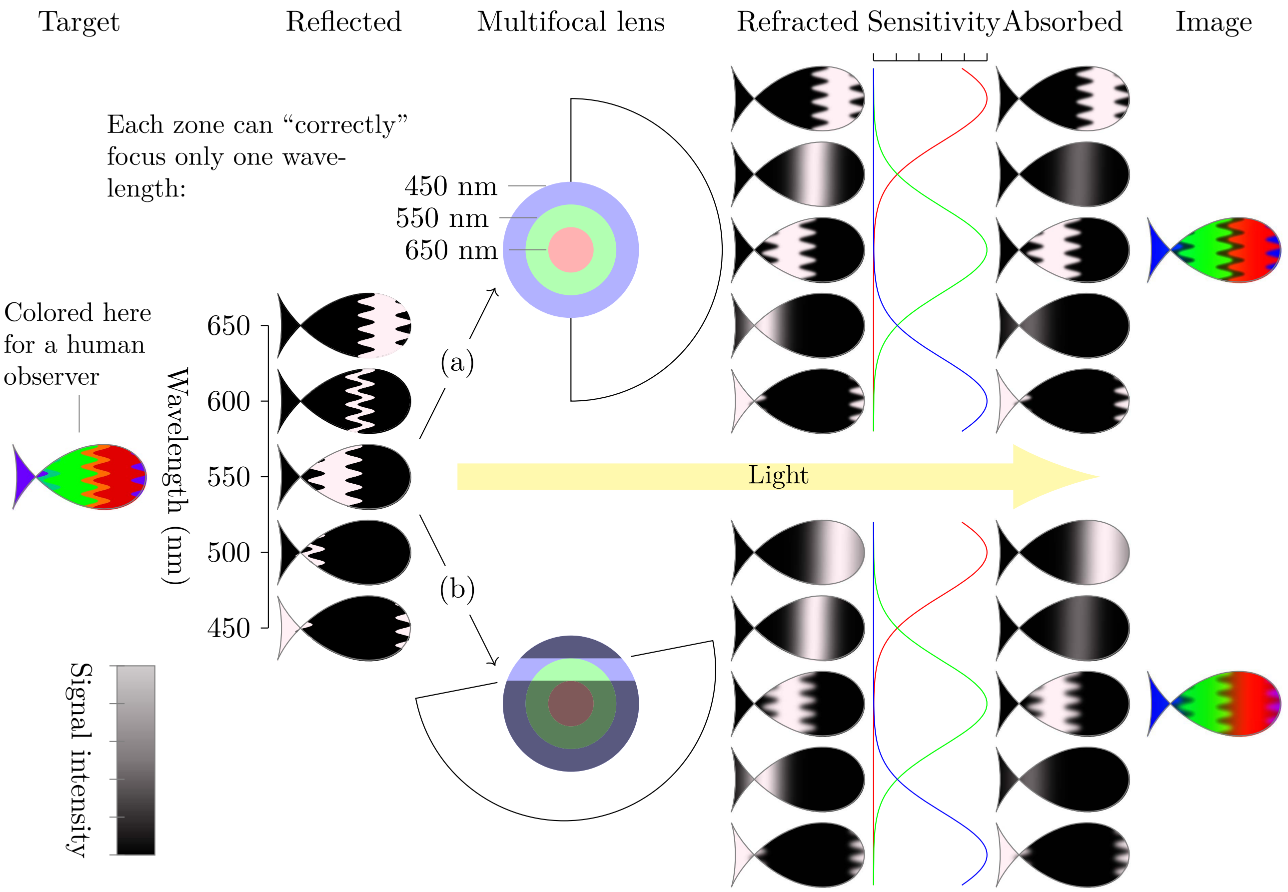


Fig. 1. Graphical simplification of the multifocal principle and how lens occlusion affects the perceived image quality. Target on the left is a fish with five jagged stripes. Each stripe reflects a different wavelength. The light is reflected from the target, gets refracted by the multifocal lens, absorbed by a trichromatic retina, and finally generates an image. The final image on the right is the three retinal channels directly translated to the red, green, and blue channels of an RGB image (approximating what the target would look like to this specific viewer). In the top part of the diagram (a) the viewing angle is perpendicular to the plane of the iris, while in the bottom part (b) the eye is accommodated (the lens is no longer in the center of the eyeball) and rotated differently so that the image falls on a peripheral region of the retina. Notice how only the wavelengths that the lens focuses correctly are sharp (this is a simplification; in nature multifocal lenses are not so discrete) while the other wavelengths are defocused (i.e., 500 and 600 nm). In (a), the retina's sensitivities are matched to the wavelengths best focused by the lens (notice how the lambda max of the sensitivity curves are aligned with the most focused images); therefore, it is those wavelengths that are most absorbed. Finally, it is the sum of these signals that provide the final image. The defocused wavelengths do not contribute to this image due to the retina's insensitivity to these wavelengths. Bottom part (b) illustrates how occlusion results in a mismatch between the retina and the lens leading to a defocused image. Here, some of the lens is occluded (e.g., the whole central zone) preventing some wavelengths (e.g., 650 nm) from being focused to the retina's plane. Because the retina is sensitive to those now defocused wavelengths they still contribute to the final image (notice how the red fish head is now defocused).

the spectral sensitivity of fishes are tuned to the spectral quality of their light environment and the visual tasks they perform [22–31]. Likewise, it has been shown that the optical properties of multifocal lenses are species specific [11,12] and functionally linked to the light environment of the organism [10–13,32–34].

In many fish eyes, which tend to have very wide fields of view, the iris can obscure large portions of the lens from rays travelling from the peripheral field of view, thus completely excluding some BEPs or changing the amount of available BEPs [Fig. 1(b)]. To us, peripheral vision may seem trivial because our natural history has driven us to evolve forward-facing eyes with a high degree of binocular overlap. However, for animals that inhabit three-dimensionally exposed environments, like fish swimming in open water, the importance of peripheral vision is reflected in the anatomy of their eyes. Fish eyes frequently protrude from the sides of their head and can provide nearly 360° views in all directions (laterally and vertically) (see Visualization 1, Visualization 2, Visualization 3, Visualization 4). The position of their eyes on the sides of their head means that the region of highest visual acuity (comparable with our fovea) is typically located near the temporal periphery of the retina providing high resolution in the forward binocular overlap zone [35]. While the retinas of these fishes see nearly a complete sphere around the fish, the light does not pass through the complete sphere of the lens because the iris blocks much of the lens at oblique angles (i.e., angles close to 0° or 180° from the plane of the iris). The relationship between BEP and wavelength (i.e., each BEP correctly focuses only one wavelength) means that such obstructions change which wavelengths come into focus at the retina and which do not. Under such conditions there may be a mismatch between the lens and the retina, and the combination no longer functions optimally [20]. Malmström and Kröger found that, in terrestrial mammals, the presence of slit pupils was correlated with the presence of multifocal lenses [16]. The authors demonstrated that the slit shape allows for a cross section of the entire lens to be used, thus making more BEPs available (across one meridian) than a circular pupil would when constricted under high light intensities. For the circular pupils in fishes, the two main factors that can result in such obstructions are (1) position of the lens relative to the plane of the iris (hereafter referred to as lens position) and (2) oblique viewing angles. It is unclear to what extent these two factors affect the available BEPs and, consequently, the focused wavelengths in the eyes of fishes. In this study, we address these questions and discuss how existing adaptations in the teleost eye may mitigate any disparities between the retina and the lens.

2. MATERIAL AND METHODS

We took photographs of the eyes of two species of freshwater fishes through a range of angles exceeding 180° around the horizontal and vertical axes, rotational photography. We chose two species: one carnivore with a pronounced aphakic space (Greek for absent lens, the absence of a part of the iris) positioned nasally (perch, *Perca fluviatilis*), and one herbivore/detritivore with no aphakic space (roach, *Scardinius erythrophthalmus*) [see Fig. 6(a) for an example of a fish eye with an aphakic space]. Both fish were donated by a local fisherman. The heads were mounted on a rotating rod and immersed in fresh water in a small glass aquarium. The orientation of rotation was measured using the position of a laser pointer attached to a rotating rod relative to a large protractor (50 cm diameter). Heads were mounted so that they rotated around the vertical or horizontal axis relative to the camera (Nikon D300, Nikon, Tokyo, Japan). Optimal illumination was achieved with a strobe (Nikon SB 900).

To better understand the implications of our observations from the rotational photography, BEP occlusion was calculated for a number of lens positions and viewing angles. We modelled the lens as a sphere and the iris as a plane with a circular aperture. Lens position was defined as the position of the lens along the axis perpendicular to the plane of the iris. The lens position varies among species and across life history stages. Typically small fishes and those that are heavily preyed upon have the lens positioned such that the plane of the iris bisects the center of the lens, thus increasing the field of view, whereas larger fishes often have the lens positioned such that the lens protrudes less beyond the plane of the iris. Such morphological differences in lens position vary by up to 0.26–0.37 R (R = radius of the lens) [36–39]. Lens position also can vary due to the dynamic lens movements that occur during accommodation, which in some species moves the lens in the plane parallel to the iris [40], while in others there can be a significant part of the motion occurring along the axis perpendicular to the plane of the iris [41]. Maximal lateral displacement due to accommodation varies greatly between 0.17 and 0.3 R [37,41,42]. The lateral displacements in our model were therefore allowed to vary between 0 and the sum of these two displacement types, 0.75 R. Viewing angles were in the range of 1°–90° (anteroposterior symmetry made the 90°–180° redundant), where the frontal direction of the fish was set to 0° and its caudal direction was set to 180°. All calculations were done in the Julia programming language [43].

The availability of BEPs was calculated as the ratio (in percent) between the unobscured part of a circle whose radius is equal to BEP and this circle's circumference (see Fig. 2 for examples and illustrations of these concepts). Describing BEP availability in this way allows us to quantify how the BEP distribution departs from the distribution found at lateral viewing angles (lens position does not affect the availability of BEPs at a viewing angle of 90°). The circular shape of the iris projects into an ellipse when viewed from angles other than 90° (blue ellipse in Fig. 2). This ellipse generally defined the shape of the obstruction by the iris. While the iris edge that was closest to the light source defined one half of the obstruction (light directed outside that edge will be obstructed by the iris), the other half was actually larger. The faraway edge of the iris did not obstruct entering beams but did obstruct exiting beams of light. Therefore, we needed to calculate the BEP that would have resulted in beams exiting the lens at the faraway edge of the iris. Due to refraction, light bends toward the optical axis as it travels through the lens, allowing some of the more peripheral light to exit the lens at a more centralized position. This meant that the edge of the obstruction was larger (more peripheral) than the actual edge of the iris and was dependent on the differences between beam entrance position and beam exit position (green line in Fig. 2). This difference was calculated for a standard spherical gradient

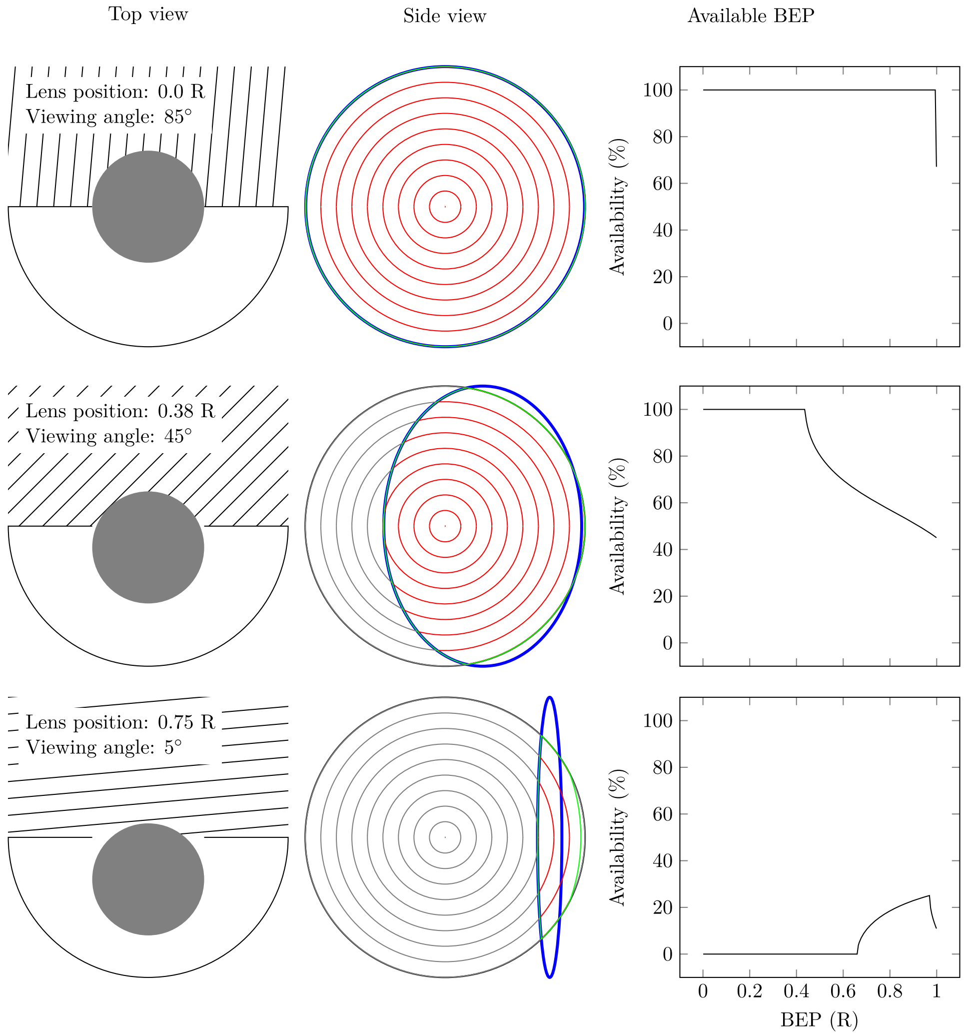


Fig. 2. Example of three combinations of viewing angles (from top to bottom: 85°, 45°, and 5°) and lens positions (from top to bottom: 0, 0.38, and 0.75 R). Left column, top view, illustrates the incoming light and the position of the lens relative to the iris. Middle column, side view, is the lens as it is viewed from the direction of the incoming light. Blue ellipse is the edge of the iris; green line defines the area through which light can refract through the lens and reach the retina; red/gray concentric circles are the possible BEPs, where the red segments are the ones that contribute to the image and the gray are the ones that do not. Right column, available BEP, availability plots of the BEPs. The x axis is BEP as a proportion of the lens radius (R), while the y axis is BEP availability in percent.

lens with a focal length of 2.33 R using ray-tracing techniques (following similar methods as in [44]).

3. RESULTS

The rotational photography of fish heads showed that a large portion of the central lens was obscured at oblique viewing angles (Fig. 3, Visualization 1,Visualization 2). This effect is not restricted to this species, the loss of central BEPs at oblique viewing angles can be observed in numerous species of fishes, as we have noted while making observations in public aquaria. The central part of the roach lens was obscured at oblique viewing angles around 30° or 150° (red line in Fig. 3). At intermediate viewing angles (between 30° and 150°), parts of the lens were obscured as well (yellow and blue lines in Fig. 3). While these measurements showed that fish lenses are partially occluded at oblique viewing angles, it is not evident how this occlusion affects the availability of incoming light and therefore BEP.

Confirming the occlusion of the lens we saw in the rotational images, our modelling showed that the availability of BEPs dramatically changed across the various combinations of lens positions and viewing angles (Fig. 4). In some cases (e.g., lens position of 0.19 R and viewing angle of 5°), some of the BEPs (e.g., BEP < 0.1 R) were missing altogether. At almost all lens positions and viewing angles, the BEP availability departed markedly from 100% availability. Indeed, the variation in BEP availabilities between the different combinations of lens positions and viewing angles was large (Fig. 4). Examples of these variations are dramatic BEP reduction (availability nearing zero) at the lens periphery, non-constant BEP availability (i.e., a stark increase or decrease of availability as a function of BEP), peak BEP availability at midrange (0.5 R) BEPs, and

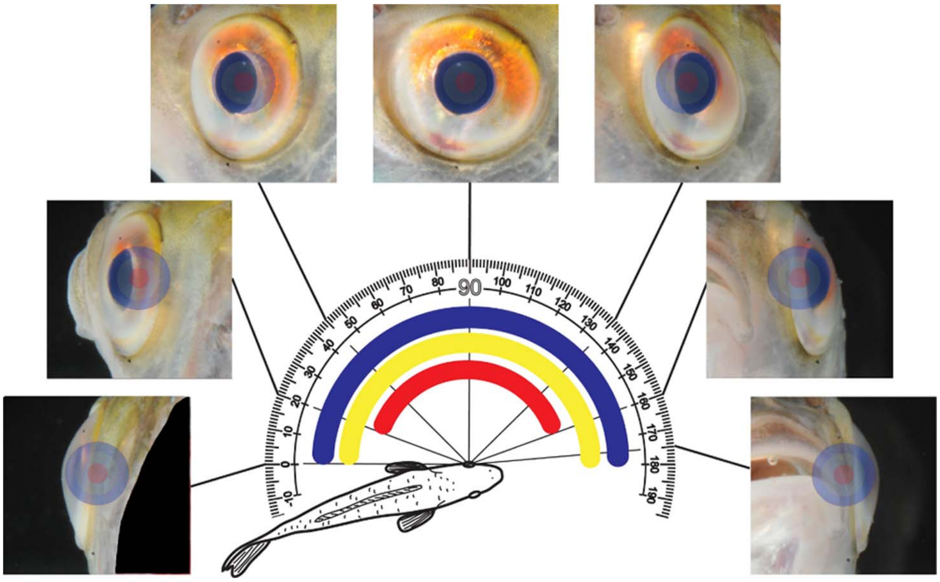


Fig. 3. Rotational photography of a fish head demonstrating the loss of central BEPs at oblique viewing angles in a horizontal rotational plane (i.e., a vertical rotational axis). We have arbitrarily overlaid colored circles on the lens to assist with visualizing the change in transmission through various BEPs; however, these are not meant to indicate spectral quality of the light best focused by these regions of the lens. For instance, note how the red central portion of the lens is occluded at angles greater than 70° from the central visual axis (90°) in the roach (*Scardinius erythrophthalmus*) and how parts of the yellow middle portion of the lens are occluded at more lateral viewing angles (see Visualization 1, Visualization 2)

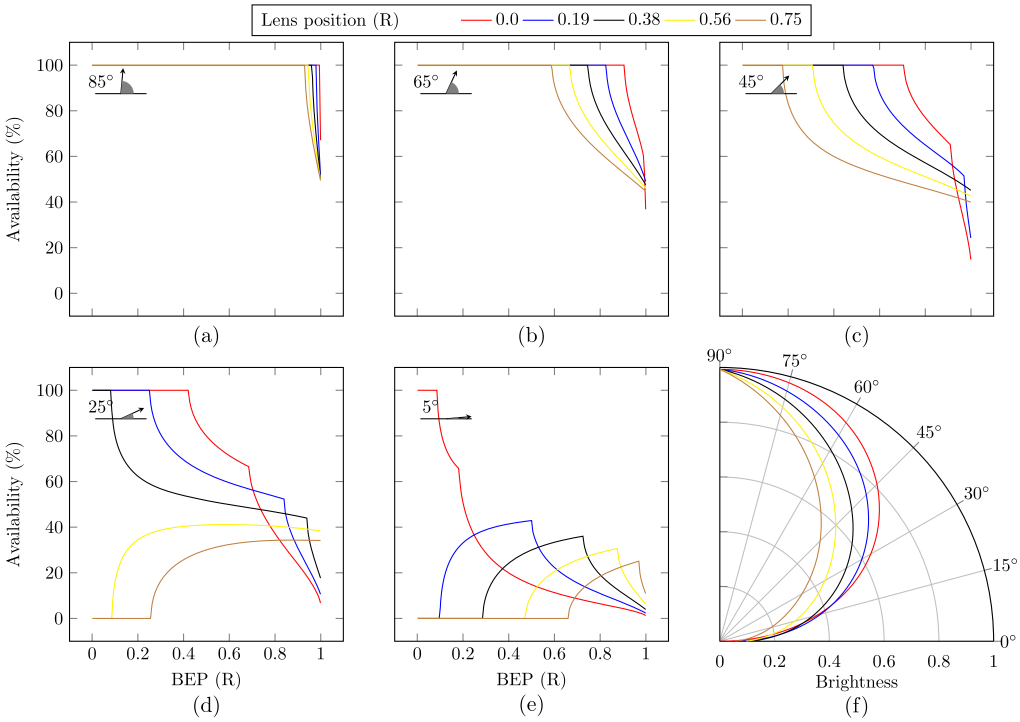


Fig. 4. BEP availability at different viewing angles and lens positions (a)–(e), and their respective image brightness (f). The x axis in the availability plots is BEP as a proportion of the lens radius (R), while the y axis is the availability (in percent) of each BEP. Panes (a) to (e) show the availability for viewing angles 85°, 65°, 45°, 25°, and 5°, respectively. The different lens positions (0, 0.19, 0.38, 0.56, and 0.75 R) are denoted with different colored lines (see legend at the top of the figure). Pane (f) describes image brightness as a function of viewing angle and lens position. The radial axis is brightness (where zero is no brightness at all and one is the maximum brightness possible), and the angular axis is viewing angle (anteroposterior symmetry made the 90°–180° redundant). The positions of the lens are color coded in the same way as in the availability plots.

central BEP sections missing altogether. While moving the lens inward decreased the amount of light entering the eye (20% less light for a displacement of 0.75 R, in combination with viewing angles other than 90°), oblique viewing angles decreased brightness even more (a viewing angle of 10° resulted in 80% less light than at 90°).

4. DISCUSSION

A. Effects on BEP Availability

Our model and the observations made from rotational photography indicated that, at oblique viewing angles and when the lens was positioned inward along the axis perpendicular to the plane of the iris, a considerable portion of the lens is not available for focusing the image onto the peripheral retina. It is important to remember that, compared with our own eyes, in which spatial resolution is much lower in the periphery, fishes often have their highest spatial resolution in the temporal periphery [35], and their best color discrimination also can be found in the same region [30]. As such, oblique viewing angles are functionally important to fish, thus making the altered BEP availability at those angles highly relevant. The change in BEP availability will affect the spectral and spatial quality of light focused onto the photoreceptors of the retina. While lens position had no effect on the availability of BEPs at a 90° viewing angle, we found that, as viewing angle increased or decreased away from 90°, the effect of lens position on the availability of BEPs increased. The same was true for image brightness. While decreased intensity can be compensated for by increasing the spatial and/or temporal summation of the photoreceptors [45], tuning the spectral sensitivity of the retina to better match the modulated spectral content of the focused image cannot be instantaneously altered. In addition to the importance of a general change in BEP availability, it is also worth noting that we saw a considerable loss of BEPs from the periphery of the lens (Fig. 4). Changes to these peripheral BEPS are more important than changes that occur to short, more central, BEPs. This is due to two main factors: (1) more light enters the lens at its periphery than near the center of the optical axis. A peripheral BEP represents a larger area through which light can enter the lens than a centralized one (the area at a given BEP equals twice that BEP). (2) The depth of field of the lens is much larger for centralized BEPs than for peripheral ones. Any changes to the availability of centralized BEPs are going to equally affect all focused/defocused wavelengths. On the other hand, even small changes to peripheral BEPs will result in a mismatch between the spectral focusing capabilities of the lens and the spectral sensitivity of the retina.

B. Implications for Image Quality

While we have successfully demonstrated that the available BEPs heavily depend on the position of the lens and viewing angle, we have not quantitatively shown how such shifts in BEP distributions affect the quality of the perceived image. While such an analysis is useful, it would require an in-depth and thorough examination of hypothetical conditions as well as a number of real-life cases. This analysis would require species in which all of the following were known: gradient of the refractive index of the lens, size and shape of the aphakic space, regional variations in spectral sensitivities across the retina, behavior, and ecological light environment. It is therefore well beyond the scope of this study, but it does present an exciting challenge for ourselves and others that delve deeper into this area. Multifocal lenses are highly sensitive to changes, specifically in their gradient of refractive index. Cichlids alter their lenses from a multifocal lens by day to a monofocal one by night. They accomplish this careful regulation by changing the concentration of dopamine (amongst other chemical factors) in their eyes [15,20,44,46]. The refractive index in the periphery of the lens changes by 10^{-4} due to this regulation. While it is unclear how equivalent minute changes in BEP availability also would affect the function of multifocal lenses, the changes we have seen in this study are dramatic and include almost any thinkable modulation to the BEP distribution (i.e., missing BEPs, low central or peripheral BEPs, or both). This occlusion is comparable in magnitude with the occlusion of a constricting circular pupil. Because circular pupils warranted the adaptation of slit pupils in multifocal lenses [16], we believe oblique viewing angles and lens movements may have driven the evolution of similar adaptations to counteract the resultant mismatch between lens and retina.

C. Possible Adaptations

We propose that two disparate adaptations of vertebrate eyes may have evolved, at least in part, to compensate for the potential loss of some BEPs. The first involves modifications to the shape of the iris, and the second involves changing the spectral sensitivity of the retina toward the retina's periphery to more closely match the wavelengths that may be best focused when some BEPs are obscured. We have focused on the eyes of fishes, where there are well-documented examples of both of these adaptations, but where previous explanations for the functional significance of these adaptations are either nonexistent or contentious.

There are two modifications to the iris that can increase the BEPs that can be accessed when light enters the eye at oblique angles. The first is an aphakic space. Many fishes possess nasal aphakic spaces, though some also possess temporal aphakic spaces or aphakic spaces in other directions (e.g., archerfish: forward and upward [30]; barracudina: upward [47]; and various others reviewed in [48]). The position of the aphakic space can be used to indicate regions of the visual field that are of particular interest to the species [30,49,50]. Aphakic spaces are common in predatory fishes and are thought to increase binocular overlap in the forward/nasal direction [49,50]. Aphakic spaces also have been proposed to increase retinal illumination [51,52]. This latter hypothesis would likely be most relevant to fishes living in the deep sea or poorly lit waters and is unlikely to explain the presence of aphakic spaces in many diurnal epipelagic fishes. In epipelagic waters, light entering the retina without first passing through the lens would not result in an image, degrading vision in the regions of the retina thus exposed. In addition to allowing for binocular overlap onto a peripheral region of the retina, we have shown that aphakic spaces also decrease occlusion of the central portion of the lens when light enters the eye at oblique angles [see Figs. 5, 6(a) as well as Visualization 3, Visualization 4]. This may be

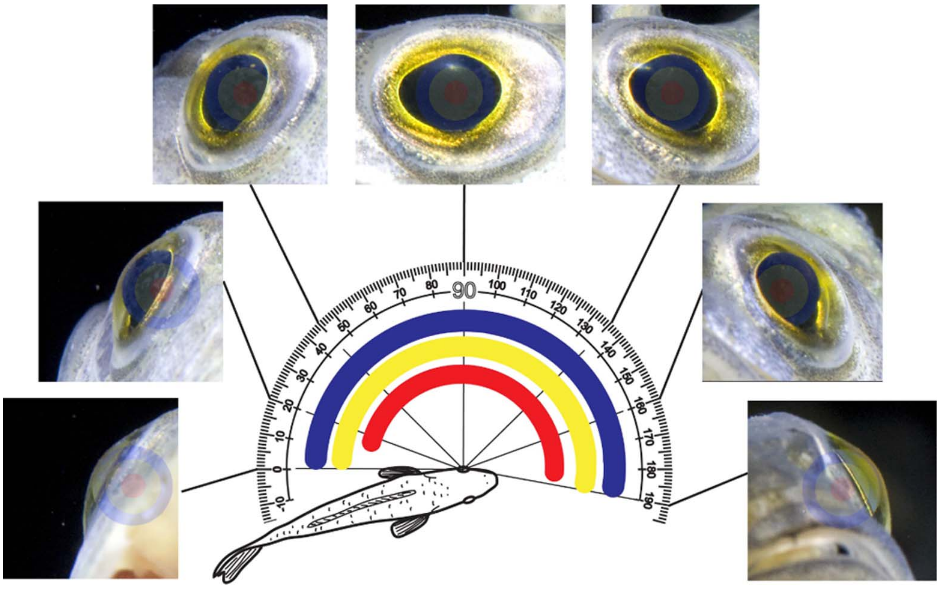


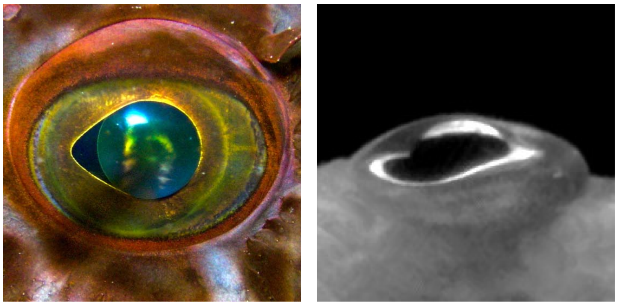
Fig. 5. Rotational photography of a fish head demonstrating the effect an aphakic space might have on lens occlusion. Perch (*Perca fluviatilis*) shows the advantage of the aphakic space at the front of the eye, which extends the use of the central (red colored) portion of the lens by nearly 30° while exposing more of the middle (yellow colored) portions (see Visualization 3, Visualization 4).

particularly important for specific regions of the retina such as a peripherally located area of high photoreceptor density (equivalent to a fovea in humans). The importance of maintaining a full gamut of BEPs is further amplified by the fact that this area of high photoreceptor density has been found to have broader spectral sensitivity in some fishes [30].

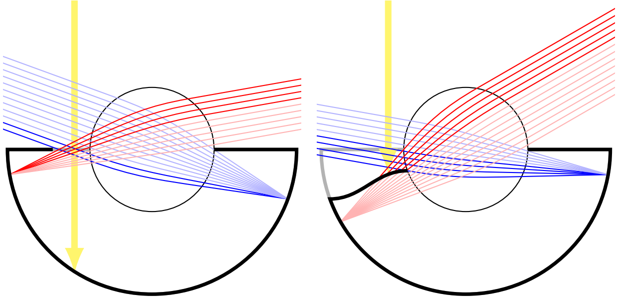
A second modification to the iris is to alter its flat planar shape by adding curvature, thus allowing the iris to more proximally connect with the lens [Fig. 6(b)]. To our knowledge such curvature of the iris has not been well documented, and we were unable to find any descriptions of a function for this adaptation. Simple geometry indicates that such curvature would increase binocular overlap in specific directions. A curved iris can address the need to focus light in the peripheral retina without the cost of allowing light to enter the eye unfocused by the lens (as occurs with an aphakic space). However, while a curvature on the frontal side of the iris, for example, will improve the optics for forward-viewing angles, it will necessarily occlude the retina for caudal viewing angles (i.e., to the retina directly behind the area of curvature). This modification affects the previously discussed iris edge that restricts the available BEPs. With a more proximal iris edge on the far side of the lens, rays that enter the lens closer to the optical axis might now exit the lens on the "outside" of the eye. This may be a more suitable compromise in high-intensity light environments where the stray (unfocused) light entering via an aphakic space may add considerable noise to the signal. As is the case with aphakic spaces, our hypothesis that a curved iris may be an adaptation to compensate for occlusion of a multifocal lens is not mutually exclusive of its potential role in increasing binocular overlap.

Modifications to the iris alter the path of light before it passes the lens and thus the extent of BEPs available to specific regions of the peripheral retina. It is, however, possible to compensate for the effect of the loss of some BEPs after light has refracted through the lens by modifying the spectral sensitivity of the retina to more closely match the spectral distribution of focused light. This hypothesis depends on the presence of different visual pigments in different regions of the retina, which would result in intraretinal variability in spectral sensitivity (IVSS), a common phenomenon among vertebrates (reviewed in [31,53,54]. Such intraretinal variations have been correlated with differences in spectral content of the visual environment and the demands of specific visual tasks in different parts of the field of view [30]. The spectral content of the animals' field of view may still be correlated to the focusing capabilities of the eye's optics as well as the IVSS (although no example of this correlation has been shown yet). Additionally, some instances of IVSS have remained unexplained: for example, the concentric rings of visual pigment opsin expression in zebrafish [55]. In the zebrafish, a gradual change in the expression of visual pigment opsins across the retina increases sensitivities to longer wavelengths toward the retina's periphery. We suggest that such variations in spectral sensitivity could be a compensation for shifts in the wavelengths of light that are well-focused on the retina at oblique angles.

We have demonstrated that occlusion of incoming light may change the spectral and spatial focusing properties of multifocal lenses. The effect of occlusion from oblique viewing angles and moderate inward movements of the lens had a dramatic effect on the availability of incoming rays (i.e., BEP). We postulated that aphakic spaces and a curvature in the iris may play a role in mitigating these effects. We further suggest that intraretinal variability in spectral sensitivity also may be linked to the changes in the spectral content of focused rays in the periphery of the retina.



(a) *Ophiodon elongatus* (c) *Toxotes chatareus*



(b) Aphakic space (d) Curved iris

Fig. 6. Effects of an aphakic space and a curved iris on the availability of BEPs. (a) Example of an aphakic space in Lingcod (*Ophiodon elongatus*). (b) Comparison between an eye with (black) and without (gray) an aphakic space. In this case, the BEP availability would increase for light coming from both directions (dark blue and dark red rays). However, stray light (yellow arrow) can now enter the eye and degrade image contrast. (c) Example of a curved iris in archerfish (*Toxotes chatareus*). (d) Illustration of incoming light rays entering an eye with a planar iris (gray) compared with an eye with a curved iris (black). The curved iris would alter the availability of BEPs by allowing more rays to enter the eye from one viewing angle (from the left; dark blue rays) than a planar iris would (bright blue rays). Rays coming from the other side of the eye (from the right; dark red) and exiting the lens would, however, be blocked by the curved iris (dark red rays). This adaptation is thus beneficial for improving vision in one direction without the costs of light leakage associated with an aphakic space (yellow arrow representing stray light is blocked by the curved iris as well as the planar one). Notice that, while these two adaptations are different, they may occur to some degree in the same species at the same time (e.g., archerfish).

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