Amphibious vision – Optical design model of the hooded merganser eye

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\textbf{ABSTRACT}

A comprehensive schematic eye model of the hooded merganser is introduced for the first time to advance the understanding of amphibious vision. It is comprised of two different configurations, the first one modeling its visual system in air (unaccommodated state) and the second one representing the case where the eye is immersed in water (accommodated state). The model was designed using available data of former studies, image analysis and the implementation of feasible assumptions that serve as starting values. An optimization process incorporating an optical design program is used to vary the starting values with the aim of finding the setup offering the best acuity. The image quality was measured using the root-mean-square radius of the focal spot formed on the retina. The resulting schematic eye model comprises all relevant optical specifications, including aspherical geometrical parameters for cornea and lens, distances between the surfaces, the gradient index distribution of the lens, the retinal specifications and the object distance in both media. It achieves a spot radius of 4.20 µm for the unaccommodated state, which meets the expectations derived by the mean ganglion cell density and comparison with other animals. In contrast, under water the determined spot radius of 11.48 µm indicates an acuity loss. As well as enhancing our understanding of the vision of the hooded merganser, the schematic eye model may also serve as a simulation basis for examining similar animal eyes, such as the cormorant or other fish hunting birds.

1. Introduction

In vertebrate eyes, the cornea and the crystalline lens have the most significant impact on the image forming process due to their refractive power. While the surrounding medium is air, the corneas contribution to refraction amounts about two thirds, leaving only one third to the crystalline lens. Considering aquatic species, the impact of the cornea is reduced to about 10% because the refractive indices of the surrounding water and the aqueous humor are similar. Therefore, the lenses of waterbound species exhibit significantly smaller radii of curvature compared to terrestrial animals eyes to compensate for this loss. Accommodation is frequently achieved by lens movement instead of lens deformation (Beer, 1894; Claus et al., 2019; Somiya & Tamura, 1973). Amphibious animals like diving birds are thus faced with the need of an extraordinary accommodation mechanism allowing them to see well in air and water, meaning the refractive power loss of the cornea occurring during immersion has to be made up for. This is not achievable with mere contraction or shift of the lens like it occurs when the terrestrial or aquatic animal eye adapts from near to distance vision. This exceptional adaptation mechanism is referred to as ‘accommodation’ in this paper. One of the first investigators of this mechanism was Hess (1910), who observed a remarkably strong lens deformation in underwater hunting birds when they were diving. Later Levy & Sivak searched for a more detailed explanation (Levy & Sivak, 1980; Sivak, Hildebrand, & Lebert, 1985). They examined mallard eyes and found that a rigid pupil is formed by the contraction of the iris sphincter muscle. Accompanied by a contraction of the ciliary body, the soft lens is forced through this pupil, creating a smaller lenticonus that shows a

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The imaging and visual qualities of the addressed species. For a Furthermore, the adapted optical eye models permit an estimation of the influence and significance of the involved optical elements. The-geometrical characteristics, which makes it possible to understand the accommodation process observed in semi-aquatic birds can be realistic. In general, realistic and sophisticated optical eye models offer the opportunity to causally link eye anatomy and its optical performance of the eye, which may differ from the natural process of an in vivo eye and may therefore not reflect the actual accommodation process.

The hooded merganser is a pursuit diving duck that feeds primarily on aquatic vertebrates and invertebrates (Johnsgard, 2010). Levy and Sivak also suggested that their eye adjustment mechanism enables the pursuit diving ducks to be emmetropic in both media (Levy & Sivak, 1980; Sivak et al., 1985).

Up to now, only qualitative evidence for this type of accommodation is available. In this paper we present a new approach to test the hypothesis that the proposed adaptation mechanism described above leads to a sufficient optical performance of the hooded merganser eye in both media – in air and under water. To accomplish this investigation, we developed a schematic eye model of the hooded merganser eye and performed optical simulations of both accommodation states, which allows us to evaluate the theoretical image quality that can be achieved under both environmental conditions. For the simulation, firstly a database for all optical relevant components was compiled, comprising in particular aspherically shaped optical surfaces (characterized by radius of curvature and conical constant), component thicknesses, distances between the components, refractive indices and a gradient refractive index (GRIN) distribution for the crystalline lens. Secondly, from the initial database an optimization process using an optical design software was carried out in which the initial parameters were varied so that finally a coherent eye model follows which is consistent with the anatomical and in particular retinal resolution characteristics. An essential question is whether it is possible to predict a focused image on the retina and with what quality, especially for the immersed case when implying the assumed adaptation mechanism. Therefore, optical modeling of the hooded merganser eye can give insight into whether the existing theory of the accommodation process observed in semi-aquatic birds can be realistic. In general, realistic and sophisticated optical eye models offer the opportunity to causally link eye anatomy and its optical-geometrical characteristics, which makes it possible to understand the influence and significance of the involved optical elements. Furthermore, the adapted optical eye models permit an estimation of the imaging and visual qualities of the addressed species. For a suitability test or a validation of the eye model in question it is not necessary that the parameters of the setup exactly match the real values – an ideal model is impossible due to the naturally occurring great variation between individual animals.

2. Methods

The process of developing an optical model or system in general starts with collecting all necessary geometrical and optical properties of the constituting components as well as the distances between the parts. Typically, not all of the parameters of this initial system are known precisely or fixed, but they have to represent a reasonable starting point for the subsequent optimization process. Next, optimization goals have to be set. For focal systems like an eye model, finding the minimum possible root-mean-square spot radius (RMS spot radius) in the focal plane is an often used and well-suited measure for evaluating image quality, since all optical aberrations induce an increase in its radius (OpticStudio, 2018). Finally, the parameters that are not strictly fixed are allowed to vary (often within a defined range or with auxiliary conditions) and the optimization routine tries to find the setup which meets the goals best (Bociort, 2003).

In Section 2.1, the acquisition of all mandatory parameters to set up the initial system is described. Starting parameters were generated by evaluating previously published work. The basic geometrical parameters were derived from Fig. 1, whereas the optical parameters were deduced from literature on different species that are assumed to bear similar adaptations. In this way the parameters of the setup exactly match the real values – an ideal model is impossible due to the naturally occurring great variation between individual animals. The process of developing an optical model or system in general starts with collecting all necessary geometrical and optical properties of the constituting components as well as the distances between the parts.
unaccommodated case. After scaling, the geometrical parameters were measured directly in the image.

Regarding the accommodated state depicted in Fig. 1(B), we used the finding that the pupil diameter decreases from the initial 4.0 mm in air down to values between 1.0 mm and 2.0 mm in water (Levy & Sivak, 1980) and assumed that the overall length of the eye remains constant when being immersed. These two indications lead to our choice of 1.5 mm for the pupil diameter of the accommodated state.

The procedure of extracting the surface shapes of the cornea and the anterior and posterior lens surfaces using Matlab is illustrated in Fig. 2 using the back surface of the lens as an example. First, a particular region of interest (ROI) for each optical element depicted in Fig. 1 has to be extracted from the original image and rotated manually by using the assumption of a symmetrical shape of the eye. The rotation angle was determined by matching the normal vector at the vertex of the visually approximated curve to the vertical image boundaries. The ROI and normal vectors of the surface are illustrated in Fig. 2(A). After rotation, each ROI was digitally enlarged, while the individually applied magnification factors were ruled by the condition that each curve of the differently-sized optical components is represented by approximately the same number of pixels, which is advantageous for the subsequent fitting procedure (see Fig. 2(B)). Next, a binarization step called Otsu’s method is performed (Otsu, 1979), which is an established thresholding method suited for gray-value images (see Fig. 2(C)). A subsequent Gaussian smoothing ensures the reduction of noise-susceptibility of the following edge-detection process according to Haralick and Shapiro (1992). The result of this procedure is a curve depicting the respective surface shape (see Fig. 2(D)). A mathematical description of the derived curve as an aspheric surface shape can be generated by applying a standard fitting algorithm to Eq. (1), which is well suited for optical design purposes and is conventionally used in respective software (for example OpticStudio, 2018).

\[
z(r) = \frac{cr^2}{1 + \sqrt{1 - (1 + k)c^2r^2}}
\]

Hereby, the z-axis is oriented along the optical axis and z(r) is the displacement of the aspherical surface from the vertex (sag height), at distance r from the axis. The parameter c describes the spherical curvature which is equal to the inverted best-fit radius \( R (c = 1/R) \), and k represents the conic constant that accounts for an aspherical shape. In order to find the vertex of the curvature a circle-fit according to Pratt (1987) was applied. Subsequently, non-linear least-squares fit to Eq. (1) was performed to extract the descriptive parameters of the curved surface. A compilation of the extracted geometrical parameters for both states of accommodation can be found in Table 1 including an estimation of the accuracy the parameters were derived with. The values reflect the apparent impression of the images: during accommodation the lens is significantly deformed resulting in a decrease of the radius of curvature of both the anterior and posterior lens surface, an increase of the axial length of the lens, and a decrease of its equatorial thickness. Correlated to the geometrical deformation of the lens, also the anterior chamber depth is reduced. We additionally assumed that the total axial length of the eye (compare with Garner & Smith, 1997) and the cornea (Levy & Sivak, 1980) remained unchanged during accommodation.

The values that could not be extracted from the images are the corneal thickness, the corneal anterior surface shape, and the refractive indices of the materials. To define suitable starting values for these parameters, a literature search was conducted with the aim of finding
Table 1
Optical and geometrical starting values for simulation and optimization including tolerances.

| Matlab aspherical surface data | AIR | WATER |
|-------------------------------|-----|-------|
| Corneal radius, posterior | R: 5.41 ± 0.54 | k: -0.26 ± 0.05 |
| Lens radius, anterior | R: 4.27 ± 0.43 | k: -0.58 ± 0.12 |
| Lens radius, posterior | R: -2.73 ± 0.27 | k: -0.72 ± 0.14 |

Matlab Distances [mm]

| Pupil diameter | 4.0 |
| Anterior chamber depth | 2.58 ± 0.26 |
| Lens thickness | 4.66 ± 0.47 |
| Vitreous chamber depth | 7.44 ± 0.74 |
| Axial length | 15.55 ± 1.56 |

Assumptions

| Cornea radius, anterior | ≥ posterior cornea radius |
| Cornea thickness [mm] | 0.40 ± 0.04 |
| Cornea refractive index | 1.376 |
| Anterior chamber Ref. index | 1.336 |
| Lens cortex Ref. index | 1.385 ± 0.005 |
| Lens core Ref. index | 1.449 ± 0.025 |
| Vitreous body Ref. index | 1.336 |
| Object distance [m] | infinity |

For \( n_{\text{eq}} \) we used the values of the merganser duck from Kreuzer and Sivak (1985). In particular, from \( n_{\text{eq}} \) at the blue and the red wavelength range \( (n_{\text{eq}}[442 \text{ nm}]=1.518±0.015; \text{and } n_{\text{eq}}[652 \text{ nm}]=1.504±0.014) \) the corresponding quantity for the reference wavelength is approximated to be \( n_{\text{eq}}[500 \text{ nm}]=1.512. \) This value was determined by applying a best-fit to Cauchys dispersion relation \( n(\lambda)=B+\frac{\lambda}{C} \) (see for example Bass, 1995) on the above mentioned indices. Utilizing \( n_{\text{eq}}[500 \text{ nm}] \) and Eq. (2), a core index of \( n_{\text{core}}=1.449 \) serving as an initial value for the subsequent simulation can be deduced. According to the accuracy the indices were given with by Kreuzer and Sivak (1985) and the fact that the respective values vary between individual animals of different age (Sivak, Ryall, Weerheim, & Campbell, 1989), the possible fitting range for the optimization process was set to 0.025. A verified GRIN distribution between the boundary values \( n_{\text{core}} \) and \( n_{\text{eq}} \) of pursuit diving ducks eye lenses is not available. Nevertheless in nature the GRIN profile for most species can be described by a second order polynomial, with the exception of human and higher primate eyes (Pierscionek, 2009). Additionally, there are studies showing slight deviations from a second order polynomial (Hoshino et al., 2011) or a better agreement with a higher-order polynomial (Jones & Pope, 2004). Therefore we chose Eq. (3) to describe the gradient index profile. The formula is later used in the ray tracing software OpticStudio (2018) which takes into account that the eye lens has a radial as well as an axial GRIN distribution due to its three-dimensional structure and the lens fibers growth (Pierscionek, 2009; Pierscionek & Regini, 2012):

\[
  n = n_0 + n_2 r^2 + n_4 r^4 + n_6 z + n_{12} z^2
\]  

(3)

with \( r^2 = x^2 + y^2 \). Here, \( x \) and \( y \) represent the lateral coordinates, \( z \) describes the axial position distance along the orientation of the optical axis, \( r \) is the radial distance from the optical axis and \( n_0 \) represents the baseline value for the index. The coefficient \( n_2 \) describes the linear part, \( n_4 \) and \( n_6 \) the parabolic part and \( n_{12} \) the higher order polynomial fraction of the gradient. For a realistic modeling accounting for the asymmetry of the lens along the optical axis, the anterior lens section (from anterior vertex to lens center) and the posterior section (lens center to posterior vertex) are adjusted individually using the constraint of a continuous transition between both at the lens center.

It is important to point out that the determination of all parameters denotes the specification of starting values for the optimization process
that is described in Section 2.2. Since their exact values are unknown, a range is specified for each value (also listed in Table 1). These tolerances are estimated to be the maximum allowable deviation resulting from the precision the values could be determined and taking into account the variation between individuals of the species. It was estimated to be 10% for all parameters apart from the conical constants. Here, due to the increased error susceptibility of the fitting procedure described in Section 2.1, the potential deviation was allowed to be 20%.

2.2. Optimization

As a ray-optical software tool we used Zemax OpticStudio® (OpticStudio, 2018) to design and optimize the two states of the eye model. The design process is analogous to the approach published regarding other species, for example humans (e.g. Liou & Brennan, 1997), the humboldt penguin (Martin & Young, 1984), the pigeon (Marshall, Mellerio, & Palmer, 1973) or goldfish (Claus et al., 2019). It starts with setting up an initial eye model using the parameters derived in Section 2.1. To select a suitable wavelength for the simulation, we considered the chromatic retinal properties of birds. In general, the retina of most avian species is comprised of four different types of cones with similar maximum spectral sensitivity (Hart, 2001). Specifically, the mallard duck (Anas platyrhynchos L.), which is related to the hooded merganser, has four individual single cones with maximum absorption peaks at 420 nm (V-cone), 452 nm (S-cone), 502 nm (M-cone) and 570 nm (L-cone) (Jane & Bowmaker, 1988). Due to the complexity of the model we omitted chromatic effects and chose a single design wavelength of 500 nm for our optimization process, which is well in the middle of the range of interest. The last input requirement is the determination of the object distance used in both configurations of the optical model. For the model in air an object distance of infinity was assumed, which corresponds to far vision and is usually applied for typical object distances larger than a few meters. Considering the immersed case, we specified a reduced object distance of 1 m, which incorporates the limited visibility induced by the rigorous change of the visual environment and correlates to the findings of Fernald (1991), Strod, Arad, Izhaki, and Katzir (2004) and White, Day, Butler, and Martin (2007). In experimental in vivo studies, the latter ones proved that the cormorant is able to detect its prey underwater only at a distance smaller than 1 m, which is therefore presumed to be a reasonable assumption also for the hooded merganser.

After establishing the initial system and defining a working wavelength, the optimization goals have to be set in the optical design Software OpticStudio®. This is done by defining a merit function including all desired optical design target values and tolerances for variable parameters. The merit function returns a value representing the deviation of the setup performance from an ideal system fulfilling all selected requirements. Therefore, carefully selecting optical target values and minimizing the overall value of the merit function is the main goal during optimization. Since the resolution in the image plane is the key parameter for the assessment of optical image quality, the main objective for the schematic eye model is to evaluate and minimize the RMS radius smaller than 1 m, which is therefore presumed to be a reasonable assumption for the hooded merganser. For comparison, according to Eq. (4) from Mitkus, Nevitt, Daniels, and Kelber (2016), the resolution limit was calculated from the posterior nodal distance PND, which is approximately 10.145 mm (see Table 2) and the ganglion cell density D of the hooded merganser. The mean peak ganglion cell density that was derived in the visual streak in the central retina of two specimens was determined to be

\[ F_{ng} = \pi^2 PND \times \frac{2D}{360} \times \sqrt{3} \]  

(4)

Since this theoretical value was determined from two retinas only, it might well be subject to variation among specimens. However, comparing the calculated resolution for the hooded merganser with the resolution of other animals eyes that can be found in the literature proves the plausibility of the value. For example, Land and Nilsson (2012) listed visual acuities of the aquila (eagle) (0.43 arcmin), humans (fovea) (0.84 arcmin), octopus (1.11 arcmin), cat (5.9 arcmin), goldfish (8.4 arcmin - a different investigation from Neumeyer (2003) revealed 11.0 arcmin) and hooded rat (60 arcmin). Lisney et al. (2013) found 2.7 arcmin for the red breasted merganser. The cormorant, which is a pursuit diving bird, was investigated by Strod et al. (2004) (3.1 ± 0.4 arcmin in air and 6.3 ± 0.3 arcmin in water) and White et al. (2007), who reported 11.8 ± 0.8 arcmin in water.

The optimization was executed for the unaccommodated and the accommodated (immersed) state separately. During accommodation, in addition to the lens deformation (external accommodation), also a redistribution of the GRIN occurs inside the crystalline lens (internal accommodation) (Trotter, 1995), which was included in the simulation as well by allowing a variation in the distribution. As a boundary condition it is ascertained that the core and cortex index are not affected by the redistribution (Garner & Smith, 1997; Kathurirangan, Markwell, Atchison, & Pope, 2008). During optimization all parameters that remain unchanged during accommodation (corneal parameters, total axial length, core and cortex refractive indices) have been matched for both models. This results in an average rather than an ideal resolution for the respective model.

For comparison, we additionally investigated the cases of a uniform refractive index and a strictly parabolic GRIN profile for the lens in the unaccommodated eye model, and the artificial situation in which we assumed the unchanged eye model but immersed in an aquatic environment instead of air. The optimized models were then further
A nearly parabolic GRIN profile was also found in other animals (Pierscionek, 2009). Nevertheless, the impact of \( n_{A4} \) is evident when comparing the resulting RMS spot size with the smallest possible value that can be gained using a plain parabolic GRIN profile (\( n_{A4} = 0 \)), which was found to be \( \sim 5.0 \) \( \mu \text{m} \). The advantage of implementing a GRIN profile becomes apparent when comparing the RMS spot size to \( \sim 8.0 \) \( \mu \text{m} \), which was derived for the case of a homogeneous refractive index within the lens. The deviation of the optimized schematic eye models’ geometric parameters from the respective values determined with the Matlab algorithm is well below 10% except for the vitreous body depth. This confirms the approach described in 2.1 for the purpose of finding suitable starting values for the optimization. A visual verification of the optimized geometrical parameters was done using CorelDRAW® (Corel Corporation, 2017), which is also shown in the right part of Fig. 3, where the surface shapes of the lens and the corneal front surface are depicted. Due to the fact that the position of the retinal layer where the incident light is absorbed is not exactly determinable in corresponding column of Table 2. The RMS spot radius is found to be 4.20 \( \mu \text{m} \) (2.12 arcmin), which is matching the expectation we derived from the ganglion cell density and is also in good agreement with the visual acuity of other species living under similar conditions. This might be regarded as an approval of the suitability of the introduced eye model, since the image quality of the optical system matches the animals resolution limit. The introduced model therefore follows the general and often observed finding in nature that different, interlocking structures and characteristics of an organism are optimally adapted to each other (Land & Nilsson, 2012; Atchison & Smith, 2000). Hence, the optimized model is well suited for further investigation.

The GRIN parameters resulting from the profile optimization for the two different sectors are summarized in Table 3. The respective GRIN distributions are graphically presented in Fig. 4 (black solid lines). Fig. 4(A) displays the curve for the axial direction of the anterior part of the lens, (B) represents the posterior part, and (C) shows the distribution in the equatorial direction, respectively. The origin of the coordinates is located in the lens core. The GRIN distribution shows an approximately parabolic profile in equatorial direction, where the closeness to the parabolic profile is recognizable by the very small coefficient \( n_{A4} \). A nearly parabolic GRIN profile was also found in other animals (Pierscionek, 2009). Nevertheless, the impact of \( n_{A4} \) is evident when comparing the resulting RMS spot size with the smallest possible value that can be gained using a plain parabolic GRIN profile (\( n_{A4} = 0 \)), which was found to be \( \sim 5.0 \) \( \mu \text{m} \). The advantage of implementing a GRIN profile becomes apparent when comparing the RMS spot size to \( \sim 8.0 \) \( \mu \text{m} \), which was derived for the case of a homogeneous refractive index within the lens. The deviation of the optimized schematic eye models’ geometric parameters from the respective values determined with the Matlab algorithm is well below 10% except for the vitreous body depth. This confirms the approach described in 2.1 for the purpose of finding suitable starting values for the optimization. A visual verification of the optimized geometrical parameters was done using CorelDRAW® (Corel Corporation, 2017), which is also shown in the right part of Fig. 3, where the surface shapes of the lens and the corneal front surface are depicted. Due to the fact that the position of the retinal layer where the incident light is absorbed is not exactly determinable in

### Table 3

GRIN coefficients for the optimized hooded merganser eye model in air and water (Grad A: GRIN for the anterior lens, Grad P: GRIN for the posterior lens).

| Coefficients | Air            | Water           |
|--------------|----------------|-----------------|
| \( n_{A0} \) | 1.389          | 1.389           |
| \( n_{A1} \) | \(-0.0031\)    | \(-0.0031\)    |
| \( n_{A2} \) | \(8.3686\times10^{-6}\) | \(9.0616\times10^{-6}\) |
| \( n_{A3} \) | 0.0413         | 0.0311          |
| \( n_{A4} \) | \(-0.0104\)    | \(-0.0034\)    |

3. Results

This section presents the simulation results including the deduced optical and geometrical parameters as well as the achieved image quality for the eye models in air and water. Furthermore, the internal changes of optical and geometrical parameters during accommodation are discussed in detail.

3.1. Optical eye model in air

The optimized schematic eye model for the unaccommodated state of the hooded mergansers eye in air resulting from the described optimization process is sketched in the upper part of Fig. 3, and all relevant parameters as well as the resulting cardinal points are listed in the table.
the images, a precise measurement of the vitreous body depth is difficult. Therefore, the occurring deviation of about 13% for this parameter is tolerable.

The results of the depth of field analysis as an essential characteristic of the visual eye properties are displayed in Fig. 5 (black solid line). The lower part of the figure shows the spot diagrams for the exemplary object distances of 1.0 m, 5.0 m, and 9.0 m. Note the different scale bars in the diagrams. The graph shows that the RMS radius remains nearly constant for a decreasing object distance from infinity down to approximately 5.0 m, and starts increasing when the distance is reduced further. The maximum calculated resolution of 4.22 µm is included in the plot for orientation. For distances below ~3.1 m the resolution reduces, illustrated by the increase in RMS spot radius. From the assumption of the suitability of the optical model, it follows that the hooded merganser is able to highly resolve objects in a distance range between 3.0 m and infinity (depth of field) without accommodation. For closer distances the image quality decreases or the eye has to be readjusted.

The results of the artificial case in which we immersed the unchanged eye model in an aquatic environment instead of air are displayed in Fig. 7. On the left column the geometrical conditions of the

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Fig. 4. GRIN profiles, for distances (in mm) from the lens center to the lens cortex, without (solid black line) and with accommodation (dashed grey line) (A) anterior axial, (B) posterior axial, and (C) equatorial.

Fig. 5. Dependence of the depth of field on the object distance, compared to the estimated theoretical RMS radius of 4.22 µm (black dashed line), for the schematic eye model in air (black solid line) and in water (gray dotted line). Below the plot the spot diagrams for 1.0 m, 5.0 m and 9 m for the unaccommodated model are shown. The green dots indicate the ray distribution on the image plane, the black circle the diffraction limit. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 6. Change of the RMS radius with increasing incident angle for the unaccommodated schematic eye model, with exemplary spot diagrams for 0° (RMS radius 4.20 µm), 5° (RMS radius 7.34 µm), and 10° (12.85 µm). The green dots indicate the ray distribution on the image plane, the black circle the diffraction limit. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
The optimized schematic eye model for the accommodated state of the hooded merganser eye immersed in water that results from the optimization process is shown in the lower part of Fig. 3. The complete illustration compares both states of the eye model and therefore visualizes which parameter changes occur during accommodation: the anterior chamber depth is reduced by ~1.0 mm, the equatorial lens diameter decreases by ~0.66 mm and the front lens radius is distinctly reduced by ~3.41 mm. Furthermore, the lens thickness increases by ~1.0 mm, and the vitreous body thickness decreases slightly. The specific parameters are summarized in the last column of Table 2. As mentioned above, the refractive indices of the core and the cortex of the lens remain constant when passing on from air to water but the GRIN profile changes. The corresponding results for the GRIN distributions are illustrated in Fig. 4 (gray dashed lines). For the axial direction of both the anterior (Fig. 4(A)) and posterior (Fig. 4(B)) part of the lens the decrease of the refractive index shows a slightly lower slope for the immersion case. This finding from the eye model is in good agreement with results presented by Levy and Sivak (1980), who identified an accommodation response of about 50 dpt by retinoscopy on living animals after medication. An even higher accommodation response of about 80 dpt was determined by Sivak et al. (1985), who identified an accommodation response of about 50 dpt by retinoscopy on living animals after medication. An even higher accommodation response of about 80 dpt was determined by Sivak et al. (1985), who examined the focal shift of enucleated eyes before and after electrical stimulation. The various results of the research approaches can be attributed to the different stimulation and measurement methods.

3.2. Optical eye model in water

The optimized schematic eye model for the accommodated state of the hooded merganser eye immersed in water that results from the optimization process is shown in the lower part of Fig. 3. The complete illustration compares both states of the eye model and therefore visualizes which parameter changes occur during accommodation: the anterior chamber depth is reduced by ~1.0 mm, the equatorial lens diameter decreases by ~0.66 mm and the front lens radius is distinctly reduced by ~3.41 mm. Furthermore, the lens thickness increases by ~1.0 mm, and the vitreous body thickness decreases slightly. The specific parameters are summarized in the last column of Table 2. As mentioned above, the refractive indices of the core and the cortex of the lens remain constant when passing on from air to water but the GRIN profile changes. The corresponding results for the GRIN distributions are illustrated in Fig. 4 (gray dashed lines). For the axial direction of both the anterior (Fig. 4(A)) and posterior (Fig. 4(B)) part of the lens the decrease of the refractive index shows a slightly lower slope for the immersion case. This finding from the eye model is in good agreement with results presented by Levy and Sivak (1980), who identified an accommodation response of about 50 dpt by retinoscopy on living animals after medication. An even higher accommodation response of about 80 dpt was determined by Sivak et al. (1985), who examined the focal shift of enucleated eyes before and after electrical stimulation. The various results of the research approaches can be attributed to the different stimulation and measurement methods.

4. Conclusion

For the broad diversity of animal eyes only a very small number of coherent optical models have been developed until now. With the present paper we contribute to narrow the existing gap between eye anatomy and findings on its visual acuity by introducing a comprehensive optical eye model for the hooded merganser for the first time, which will expand the understanding of amphibious vision. The developed schematic eye model contains all relevant geometrical and optical parameters and it was used to test the hypothesis that the accommodation mechanism assumed by Levy and Sivak (1980) is possible and leads to a sufficient image quality in both accommodation states.

As the results have shown, the visual acuity of 2.12 arcmin that was determined in the unaccommodated state is similar to the one determined from the retinal characteristics of the hooded merganser. The simulation also shows that with the strong lens deformation assumed by Levy and Sivak (1980), it is possible to obtain an image in the retinal layer. However, for the immersed case the achieved resolution is reduced to 6.27 arcmin, which means that the hooded merganser has about three times lower visual acuity under water than in air. Thus, this accommodation process cannot be considered adequate to compensate for the decrease of the refractive index.
for the loss of the corneal refractive power upon immersion. However, his finding correlates with the studies of other species Strod et al. (2004) and White et al. (2007), who also found a lower resolution for the cornean in water (6.3 and 11.8 arcmin) compared to air (3.1 arcmin). Therefore, it is possible that the hooded merganser holds further ecomorphological adaptations of the visual system, which might be beneficial for underwater vision (as was suggested by Lisney et al. (2013)). Likewise it has to be considered that, as was assumed by Martin, White, and Butler (2008) and White et al. (2007) for the cor-

Some remarks on potential uncertainties have to be added: the ini-
tially set up eye model relies on the findings of Levy and Sivak (1980), who used two different eyes for illustrating the two accommodation states. Additionally, the amount of drug induced accommodation has not been verified to match the relevant natural conditions. Further-

Nevertheless, the possible discrepancies are not substantial to the
introduced eye model, which can now serve as a simulation basis that can be adjusted according to new findings. Even though the hypothesis of a sufficient optical performance cannot be confirmed for both accommodation states, the resulting schematic eye model operates greatly according to expectations based on the studies that are available on data and behavioral studies of amphibious and semiaquatic animals with predatory lifestyles. In summary, the introduced eye model inte-
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CRediT authorship contribution statement

I. Urban: Conceptualization, Methodology, Writing - original draft, Writing - review & editing. Xavier Uwurukundo: Software, Writing - original draft. Daniela Stumpf: Writing - review & editing. Robert Brüning: Writing - original draft. Andreas Reichenbach: Supervision. Mike Francke: Writing - review & editing. Robert Brunner: Supervision, Conceptualization, Writing - original draft, Writing - review & editing. Ilka Urban: Conceptualization, Methodology, Writing - original draft, Writing - review & editing. Xavier Uwurukundo: Software, Writing - original draft. Daniela Stumpf: Writing - review & editing. Robert Brüning: Writing - review & editing. Robert Brunner: Supervision, Conceptualization, Writing - original draft, Writing - review & editing.
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