Refractive Error and Vision in Fishes

Abstract. The eyes of living immersed herring and silversides are farsighted and require greater hypermetropic correction for lateral vision than for anterior vision. Comparisons of lens-to-retina distances in frozen material with focal lengths of lenses are consistent with the degree of hypermetropy found by retinoscopy.

Measurements of refractive error on the alewife, *Alosa pseudoharengus,* and on the silversides, *Menidia menidia,* were determined during studies of the function of vision in the orientation of schooling fishes. These fishes are farsighted (hyermetropic). Subsequently, a number of other species (schooling and nonschooling) were examined. They, too, are farsighted (*1*).

Refractive error was measured with a streak retinoscope, an instrument commonly used by ophthalmologists, and the procedure for standard retinoscopy (with a plano mirror) was carried out on live fish. The refractive error (accommodation) in the eye was measured to the nearest diopter with a trial lens set (*2*), and the correction necessary to make the eye normal sighted (emmetropic) was obtained. Measurements, in most cases, were made from a position lateral to the fish, along the optic axis of its eye, with the trial lens outside the aquarium approximately 25 mm from the fish's eye and 1 m from the observer's eye. In a few cases, measurements were made from a position anterior to the fish's eye with the light beam pointed nearly parallel to the body axis (Fig. 1). During retinoscopy some fish were freely swimming in the tank and others were restricted to one part of the tank. The results of retinoscopy of several species are given in Table 1.

Retinoscopy from a position anterior to the eyes of 11 *Menidia* gave an average refractive error of +5.9 ± 2.2 diopters (standard error); the same fish show an average refractive error of +13.8 ± 1.9 diopters (S.E.) from the lateral view. Similarly, in the alewife, retinoscopy from the anterior position gave an average refractive error of +3.57 ± 1.46 diopters (S.E.), and from the lateral view an average of + 8.4 ± 0.5 diopters (S.E.). Two of these alewives, in extreme lateral body flexion during restraint, showed an accommodation of −1 to −3 diopters during measurements from the anterior view, and one other alewife showed a measurement of +18 diopters. The generally lower refractive error measured from the anterior view is not yet understood because anatomical studies predict an even higher positive refractive error from the anterior view than from the lateral view; it is not possible to interpret these results without further experimentation. Pumphrey (*3*) assumes a greater distance from lens to posterior retina than from lens to lateral retina for trout eyes but gives no actual measurements. His calculations are interesting but rest on the untested assumption that the image in the trout eye is actually in focus. It remains to be seen whether retinoscopic observations will substantiate his calculations for the trout eye. The refractive error (lateral) of dead alewives and dead silversides is greater than that of living specimens. Fourteen alewives showed an average refractive error of +12.3 diopters with a standard deviation of 2.45 diopters, and five silversides an average error of +13.4 diopters with a standard deviation of 4.8 diopters. The high variance of the data is to be expected because the fish show a great range of accommodation, frequently changing 6 to 7 diopters, and occasionally as much as 10 diopters during retinoscopy. Measurements of refractive error are instantaneous and do not necessarily reflect the range of accommodation possible in the fish.

In addition to measuring refractive error in living fish, the focal length of the crystalline lens was measured on extirpated lenses suspended in Ringer's solution. Image distances of objects at infinity were measured by using a compound microscope (without a substage condenser) as an optical bench. An object was placed 5 m from the lens, and the distance behind the center of the lens where this object came into sharp focus was estimated to be the focal length of the lens. In the alewife, the average focal length of 19 lenses was 6.04 mm (range 5.2 to 6.9 mm) with a standard error of 0.13. The average diameter of 10 lenses was 5.6 mm (range 4.36 to 6.92 mm) with a standard error of 0.78. There was great variation in lens diameter among many fish of similar size.

Anatomical sections of alewife heads were made from fish that had been quickly frozen alive, in Dry Ice and acetone. Various lens-to-retina distances were measured directly, through a number of different planes, on photographs of the frozen sections. Although it is not completely certain in view of the small sample size, measurements of ten sections indicate an average lens-to-retina distance of 5.8 mm with a standard error of 0.12 mm, making the average lens-to-retina distance about 0.2 mm shorter than the average focal

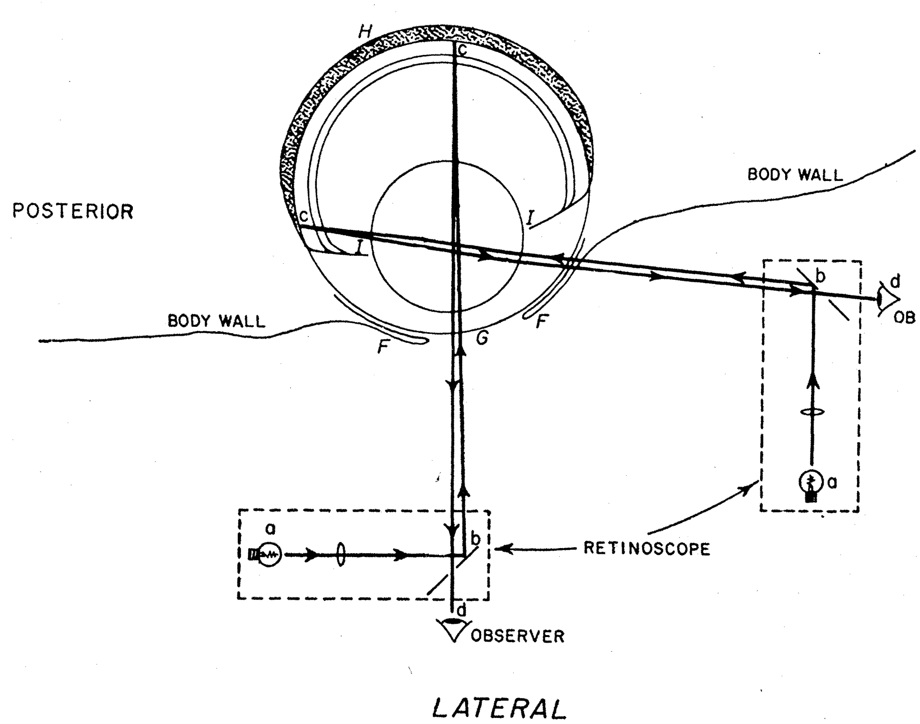

Fig. 1. Optical paths employed in lateral and anterior retinoscopy of fish eyes. The light ray *abc* is projected from the retinoscope to the argentea, *c,* and the ray *cd* is reflected to the observer's eye. *F,* the adipose lid; *G,* the cornea; *H,* the sclera; and *I,* the iris.

Table 1. Refractive error of living immersed fishes. The average hypermetropy for left and right eyes (with standard errors, S.E., for *Alosa* and *Menidia*) or the average hypermetropy for either eye (eye not determined) is given.

Species	Observations (No.)	Hypermetropy (in diopters)				
		Left eye	S.E.	Right eye	S.E.	Either eye
Alosa pseudoharengus (alewife)	23	7.9	3.38	8.02	3.10	
Menidia menidia (silversides)	33	14.57	5.14			
Menidia menidia (silversides)	36			15.80	5.65	
Paralichthys dentatus (summer flounder)	7	3.8		4.3		
Prionotus carolinus (searobin)	5	4.7		4.4		
Pomatomus saltatrix (bluefish)	3	6.7		6.3		
Carcharhinus longimanas (whitetip shark)*	1	0		3		
Myctophid (lantern fish)*	1	20		20		
Coryphaena hippurus (dolphin)*	1	4		4		
Seriola sp. (amberjack)*	1	5		6		
Caranx chrysos (blue runner)*	1	8		8.5		
Xiphius gladius (swordfish, large)*	1			4		
Xiphius gladius (swordfish, small)*	1	5		6		
Prionace glauca (blue shark)*	1	7		7		
Alepisaurus sp. (lancet fish)*	1	6		6		
Mola mola (ocean sunfish)*	1	8		8		
Pseudopleuronectes americanus (winter flounder)†	3					10
Hemitripterus americanus (sea raven)†	2					7.5
Stenotomus sp. (scup)†	1					4 to 5
Macrozoarces americanus (ocean pout)†	1					3 to 4
Brevoortia tyrannus (Atlantic menhaden)	1					4
Squalus acanthias (spiny dogfish)†	1					6
Mustelus canis (smooth dogfish)†	1					8
Raja sp. (skate)†	1					8

* These observations were made on cruise 265 of *R/V Bear*. † These observations were made at the Aquarium of the Fish and Wildlife Service, Woods Hole, Mass.

length of the lens. In two sections the distances from lens center to anterior and posterior retinal surfaces are approximately 10 percent greater than the distance from lens center to the lateral retinal surface. This observation is consistent with our retinoscopic observations parallel to the body axis of the fish and supports the observations of Pumphrey (*3*) on the ellipsoidal shape of trout retinas.

Our results contradict the currently accepted opinion stated by Walls (*4*) and Brett (*5*) that fish are near-sighted (myopic). These authors rely heavily on the conclusions of Beer (*6*) who found fish to be far-sighted by retinoscopy; nevertheless "he discarded these results in favor of a theoretical analysis of the dioptric system of the eye" (*7*, p. 638). Beer applied a theoretical equation relating focal lengths, retinoscopy observations, lens diameter, retinal thicknesses, and the like, which relied upon the assumption that retinoscopic reflection occurred from the front of the retinal surface instead of from the rear thereby introducing an error. Consequently, he concluded that fish are myopic. His assumption about the reflecting surface of the retina is demonstrably incorrect. We have found that reflection comes from behind the retina by examining the eye through a +10-diopter lens with a dissecting microscope equipped for vertical illumination from above. Evidently the reflection is derived from the guanine pigment layer behind the visual cells. On the other hand, Rochon-Duvigneaud (*8*), Verrier (*9, 10*), and Barron and Verrier (*11*) reported that all the species they examined were hypermetropic, and moreover, Verrier (*10*) found that upon replacing the retina with a screen, the image focused beyond the screen.

In addition to the retinoscopy results, there is evidence to suggest that fishes see what we would consider rather poor images. Very few teleosts have a fovea (*4, 8*). Most species have large cones and many have double cones (*4, 12*) which are distributed in a mosaic pattern among the rods. A greater number of cones would be covered by a defocused image than a sharply focused image.

Is the far-sighted eye one part of the adaptive mechanism for seeing in water? In water, light intensity undergoes multiple scattering in all directions thus providing a hazy background against which any image would need to be resolved; under these conditions a sharply defined image would be extremely difficult to obtain. Rather than acuity, therefore, contrast enhancement and motion perception would be advantageous. The mosaic distribution of teleostean cones would permit contrast enhancement. Wagner *et al.* (*13*) have demonstrated in goldfish retina the reciprocal inhibition of adjacent cone cells, a mechanism thought by Hartline and Ratliff (*14*) to produce contrast enhancement in *Limulus*, the horseshoe crab. Motion perception is a corollary of this contrast enhancement. Thus the teleost eye may be capable of perception of small movements and of sharpened contrast. This kind of vision may be highly adaptive in schooling behavior (*15*).

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References and Notes

1. The refractive error in each of two stennellid porpoises was −3 diopters in air (near-sighted) and +5 diopters under water (far-sighted). Four squid (*Ommastrephes* sp.) had no refractive error under water but had a −3-diopter error in air.
2. We thank Dr. William Stone, Jr. (Massachusetts Eye and Ear Infirmary), for the use of his retinoscope and trial lens set.
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