

Chapter 3

Optical variability of the fish lens

Jake G. Sivak

3.1 INTRODUCTION

The vertebrate eye is a sophisticated optical instrument which appeared after millennia of evolutionary development. Its optical components, cornea, lens and humours, transmit and focus light energy on a photosensitive transducing element, the retina.

The crystalline lens of the vertebrate eye is a cellular structure that develops embryologically as a vesicular invagination of the surface ectoderm. Initially, the lens vesicle is a hollow sphere formed by a wall of epithelial cells. The cells of the posterior half of the sphere elongate (the primary lens fibres) to fill the lumen of the vesicle. Subsequent cell multiplication, both embryonic and post-embryonic, takes place around the lens equator, with new cells elongating (the secondary lens fibres) and compressing the old lens material toward the centre. The result is the formation of a lens of variable density and variable refractive index, that of the centre being higher than that of the periphery.

The equatorial location of new lens growth and the fact that lens cells must taper anteriorly and posteriorly in order to articulate with the tips of adjacent cells, makes it reasonable to expect the lens to assume a more and more elliptical shape as it grows (Figure 3.1). Indeed this is the common developmental description of the human lens (Scammon and Hesdorffer, 1937; Duke-Elder, 1958; Tripathi and Tripathi, 1983), and no other explanation for lens shape is given.

The central location of the lens within the eye, and the development of new cells around the equator through life, mean that older tissue is compressed toward the centre rather than being disposed of. This has important consequences in terms of physical changes associated with age: presbyopia (loss of accommodation) and cataract (loss of transparency).

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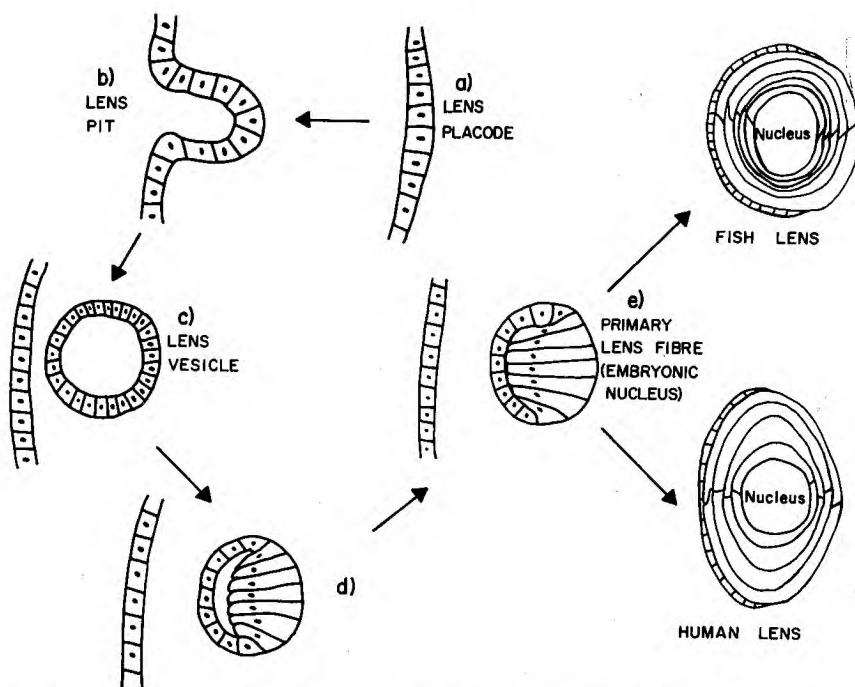


Figure 3.1 Schematic representation showing developmental sequence of lens formation.

While this developmental sequence is common to all vertebrate lenses, the ultimate shape and refractive index distribution of the lens varies considerably among species. The primary reason for this variation is the fact that the cornea of the vertebrate eye acquires refractive significance when the eye is in air but not when the eye is in water (Sivak, 1980).

The cornea is a relatively thin, avascular, transparent structure consisting of two curved and fairly parallel surfaces. Its refractive function is dependent on the existence of media of unequal refractive index in front and in back, a condition met when the eye is in air but not when it is in water. Clearly, the aquatic habitat of ancestral vertebrates limited the original function of the cornea to that of a transparent window.

Since the lens is the only refractive element of an aquatic eye, present-day aquatic species, be they fishes or other aquatic vertebrates (e.g. sirenians, cetaceans), are said to possess a spherical or nearly spherical crystalline lens of high refractive index. The focal length of these lenses has been described as a constant ratio (Matthiessen's ratio) of focal length to lens radius of *c.* 2.55 : 1 (Walls, 1942; Pumphrey, 1961; see also Section 2.2). The refractive

index is thought to drop continuously (and parabolically, according to Matthiessen, 1880) from the centre to the periphery so as to produce a lens with little or no spherical aberration. How the fish lens maintains the spherical shape of the embryonic nucleus is unknown.

The typical aquatic cornea has a relatively flat shape, presumably an adaptation related to the need for streamlining body shape in a dense medium such as water (Jamieson, 1971). The variety of accommodative mechanisms described or suggested for aquatic vertebrates always involve lens movement (Beer, 1894; Franz, 1934; Walls, 1942; Sivak, 1980).

When the cornea is exposed to air, as in the case of vertebrate evolution to a terrestrial life style, it often becomes the dominant refractive element. This is simply due to the substantial refractive index difference between air and the aqueous humour of the eye. In addition, the radius of curvature of the terrestrial cornea is relatively short, often shorter than that of the globe as a whole, as in the human case. This factor may be related to the need for a significantly arched configuration in order to maintain a smooth refractive surface in air. Whatever the reason, it adds to the refractive importance of this structure, but only when the eye is in air. The lens of a typical terrestrial vertebrate is usually elliptical in shape (diameter > thickness), softer in consistency and of lower refractive index. Terrestrial species usually accommodate by changing the shape of the lens.

The spherical shape of the fish lens, and speculation regarding the effect of a variation in refractive index on its focal properties, attracted the attention of a number of notable nineteenth-century scientists including such figures as Brewster (1816), Maxwell (1854) and Matthiessen (1880, 1881, 1882). The writings of Luneberg (1944) and Pumphrey (1961) represent continued theoretical and experimental interest in the optics of the fish lens in the present century.

It is important to note that since the lens of the fish eye is its only refractive element, lens optical quality represents that of the whole eye. Furthermore, the fish pupil is usually immobile. Light control in these eyes takes place by means of retinomotor mechanisms involving cellular changes at the level of the retinal pigment epithelium and/or the photoreceptors themselves (Walls, 1942; Ali, 1975). Thus the fish eye operates at low *f*-stop levels at all times and the iris cannot shield the retina from aberrant light rays. In some species, pupil diameter may actually exceed lens diameter (Sivak, 1980).

The fish lens is particularly useful for the study of the aplanatic nature of the lens (control of spherical aberration), since the measured aberration cannot be neutralized by corneal aberrations of opposite sign. In addition, since the fish lens is spherical, lens shape is not a factor in the control of spherical aberration. The variation in lens refractive index which results from the sequence of continual lens development is the only means by which spherical aberration is minimized. Finally, fish accommodate by moving the

lens (Chapter 2) and therefore accommodative effects on spherical aberration need not be considered.

Since 1970 there has been an asymptotic increase in the number of reports dealing with the optical nature of the fish lens. The review which follows will examine this period by concentrating on three related directions of inquiry: (1) to what extent is a spherical lens shape universal among fish? (2) is Matthiessen's ratio (focal length : lens radius) a constant value among fish? (3) is the refractive index distribution of the fish lens smooth and continuous, and to what extent is spherical aberration controlled?

3.2 LENS SHAPE

Reviews such as those of Walls (1942), Duke-Elder (1958) and Pumphrey (1961) make it clear that a spherical shape is the most appropriate design for the lens of an aquatic vertebrate. Indeed, Pumphrey includes cephalopods, thereby encompassing all simple eyes that operate in an aquatic medium.

While it appears that most teleost lenses are spherical or nearly so (Matthiessen, 1880), it is also apparent that many exceptions exist and that lens shape should not be taken for granted. A number of such exceptions exist, for example, among the elasmobranchs (Figure 3.2) (Gilbert, 1963; Sivak, 1978). Thus, the equatorial diameter of the lens of the bluntnose stingray, *Dasyatis sayi*, exceeds lens axial diameter (thickness) by 18% (Sivak, 1976). Flattened lenses are found in other stingrays as well (Sivak, 1978). Among the sharks, the equivalent values are 15% in the nurse shark, *Ginglymostoma cirratum*, 16% in the sandbar shark, *Carcharhinus milberti*, and 12% in the bull shark, *C. leucas* (Sivak, 1978). However, the lens of the spiny dogfish, *Squalus acanthias*, is almost spherical, with diameter exceeding thickness by only 4%. In a skate, *Raja eglanteria*, the difference is even less (about 2%, Sivak, unpublished).

The elasmobranch eye, in so far as it does not follow the typical teleost pattern, is unusual for another reason. Whereas the teleost pupil is generally immobile, the elasmobranch pupil commonly responds to varying levels of illumination, even though retinomotor mechanisms may exist as well (Kuchnow and Martin, 1970). The rapidity of pupil constriction and dilation in certain species (as little as 5 s) agrees with a level of neuromuscular development found only in the iris of higher vertebrates. The focal properties of the elasmobranch lens have been almost entirely ignored. Given the variation from the spherical model for teleost eyes and the fact that much of the lens is hidden by the iris, at least in diurnal conditions, measures of refractive index distribution and spherical aberration may prove to be very different from those found for teleost lenses.

Probably the best-known example of a non-spherical teleost lens is that of

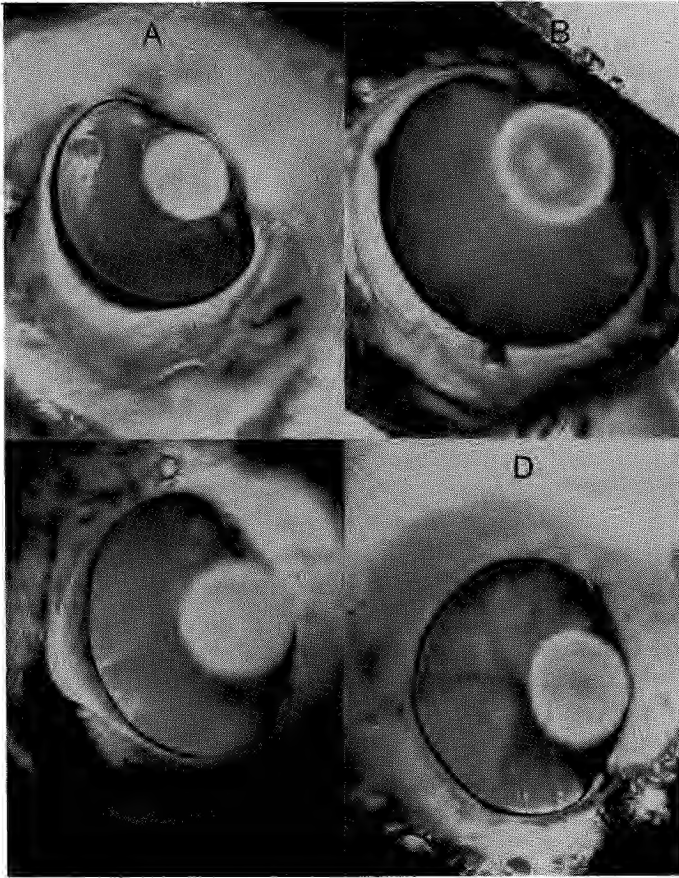


Figure 3.2 Sagittal cross-sections through the eyes of the following species of sharks: A, nurse shark, *Ginglymostoma cirratum*; B, bull shark, *Carcharhinus leucas*; C, spiny dogfish, *Squalus acanthias*; D, sandbar shark, *Carcharhinus milberti*. (2–3 \times , reproduced with permission from Sivak, 1978).

Anableps anableps, the so-called four-eyed fish (Figure 3.3). *Anableps* spends much of its time swimming at the water surface of estuaries with the upper half of each eye exposed to air (Klinckowstrom, 1895). A horizontal strip divides the cornea at the water-line, while the pupil is split by the iris into upper and lower apertures. The lens is oval in shape, with the long axis corresponding to the ventral (aquatic) pupil axis and the short axis corresponding to the upper (aerial) pupil axis. Schwassmann and Kruger (1965) recorded separate aerial and aquatic projection maps of the retina on the optic tectum of *Anableps microlepis*. Lens power along the long (aquatic)

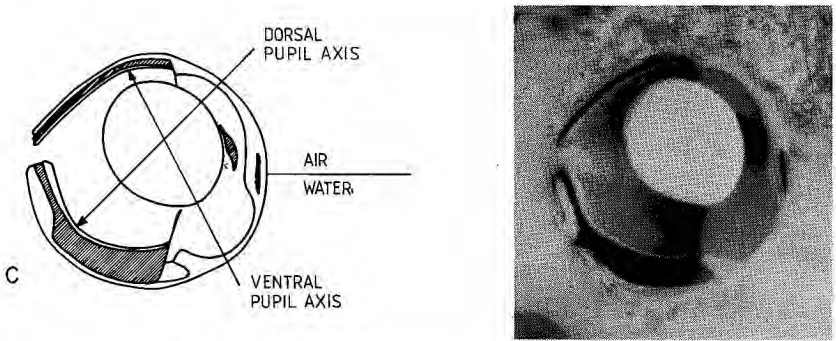


Figure 3.3 Drawing and frozen section of the eye of *Anableps anableps* showing non-spherical lens (reproduced with permission from Sivak, 1980).

axis is such that the surface of the retina is almost in contact with the posterior pole of the lens. Refractive measures support the view that the double optic paths of the *Anableps* lens are designed to compensate for the refractive power contributed by the upper portion of the cornea when it is in air (Sivak, 1976).

Anableps is probably one of several teleosts in which the lens departs from the typical spherical shape for reasons related to a need for multiple optic axes. Saidel (pers. comm.) has noted that the lens of *Pantodon buchholzi* (Teleostei, Osteoglossiformes) is not spherical. As in *Anableps*, this lens may be an adaptation related to simultaneous air/water vision.

Munk (1986) describes relatively small oval lenses of two mesopelagic teleosts, *Trachipterus trachipterus* and *T. arcticus* (the ribbon or deal fish), in which lens thickness (axial diameter) is greater than equatorial diameter; i.e. the long axis of the ovoid coincides with the equatorial axis rather than the pupil axis of the eye. According to Munk, these lenses are multifocal devices designed for the abnormally shallow retinal cup located in the head of a laterally compressed fish.

Munk (1984) also describes flattened (non-spherical) lenses with equatorial diameters greater than thickness (axial diameter) in several species of pelagic deep-sea teleosts. Munk theorizes that such eyes are underpowered (hyperopic) in that lens focal length is probably longer than the distance between the lens and the retina. Presumably good visual resolution ability is not important to these species. However, this view may be premature given the fact that flattened lenses are common in elasmobranchs such as the bluntnose stingray, *Dasyatis sayi*, in which vision appears to be an important sense. Clearly, lens shape alone cannot indicate whether lens focal properties are appropriate or inappropriate. Measurements of refractive properties and refractive index distributions in living, or at least fresh, specimens are required.

There are numerous examples in the comparative literature indicating that lens shape is in fact determined by the overall refractive needs of the species in question. Intertidal fish, *Periophthalmus* for example, may have 'aerial' lenses, i.e. flattened lenses in which lens thickness is less than lens diameter (Graham, 1972). Vision may be poor in water.

Perhaps the most obvious example of lens refractive function is the change in shape of the amphibian lens during metamorphosis from aquatic larvae to terrestrial forms (Sivak *et al.*, 1985). Sivak *et al.* examined the rate and extent of ocular metamorphic change in five species with widely varying life histories. The results show that the larval eye is teleost-like in all species. The lens is spherical, or nearly so, in shape and is in close proximity to the relatively flat cornea. However, the adults of the same five species show widely varying metamorphic change, both in rate and extent of change. For example, the lens of the toad, *Pelobates syriacus*, is flattened (equatorial diameter 21% greater than axial) and the eye is subject to a long metamorphic period (20 weeks). By comparison, the lens of the bullfrog, *Rana catesbeiana*, is less flattened in the adult (12.5%) but the change takes place over a short (24 h) period just before the animal moves onto land. A similar rapid change is found in *Salamandra salamandra*. In *Notophthalmis viridescens*, a urodele which undergoes a second metamorphosis back to water after a land period, the lens changes shape twice (spherical to flattened to spherical). Finally, in the clawed frog, *Xenopus laevis*, which remains aquatic in behaviour as an adult, the lens maintains its spherical shape.

The manner in which variation in lens shape is brought about is not known. It may be due entirely to new lens growth, as brought about by a temporary increase in the rate of equatorial cell mitosis, or it may be the result of a change in volume and configuration of existing cells. The fact that the adult lens of certain amphibians is not larger than that of the larval form supports the latter explanation.

3.3 RELATIVE FOCAL LENGTH (MATTHIESSEN'S RATIO)

While the ratio of focal length to lens radius, Matthiessen's ratio, is taken to be a constant 2.55 : 1 by Walls (1942), Pumphrey (1961) and others, Matthiessen (1880, 1881, 1882) actually reported wide focal variations and 2.55 can only be considered to be a representative figure. Of species examined by Matthiessen, the ratio varied from 2.40 to 2.82 : 1, a considerable spread. Furthermore, great variations were noted among individuals of the same species (see also Chapter 2).

Considerable experimental attention has been directed toward the direct measurement of fish lens focal length by using either an optical-bench approach, in which focal distances are measured for given object conditions,

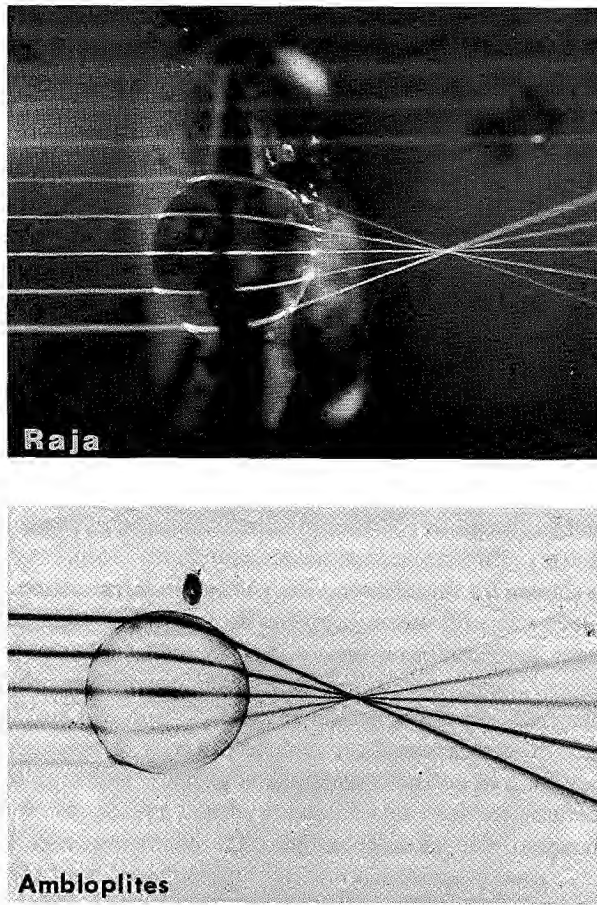


Figure 3.4 Examples of differences in relative lens focal length (Matthiessen's ratio). Skate, *Raja eleganteria*, ratio = 2.57; rock bass, *Ambloplites rupestris*, ratio = 2.27. An array of parallel laser beams (helium-neon) are projected through lenses in a physiologically life-like solution. Lenses are 5–6 mm in diameter.

or by photographing lens refractive effects on collimated incident light. The optical-bench approach is usually carried out with a compound microscope, using either a self-contained or an external micrometer control to measure the amount of movement of the objective when focusing on a portion of the lens and the image of the target. Baylor and Shaw (1962) reported focal lengths and diameters for 19 alewife, *Alosa pseudoharengus*, lenses which give an average ratio of focal length : lens radius of 2.16 and a range from 1.99 to 2.38 : 1. Similar measures by Charman and Tucker (1973) indicate a ratio of

2.35 : 1 for the goldfish, while Sadler (1973) reported Matthiessen ratios of 2.429 : 1 for the saithe, *Gadus virens*, and 2.561 : 1 for the cod, *Gadus morhua*. Kreuzer and Sivak (1984) report average ratios varying from 2.21 to 2.43 : 1 in 13 teleost species (Figure 3.4).

The fact that the focal length of any lens may vary with wavelength (chromatic aberration) and/or position of the incident beam on the lens (spherical aberration) suggests that a single focal characteristic for a lens may be impossible. Sroczyński (1975 a and b, 1976, 1977, 1979 a and b, 1981) modified the microscope-optical-bench method by making it possible to measure focal lengths for concentric lens zones from the periphery toward the centre. This measure, spherical aberration, is discussed in Section 3.4. The point to be made here is that Sroczyński reported that even if measures of focal length are restricted to a specific zone of the lens, Matthiessen's ratio (relative focal length) varies among species and among individuals. For example, the lowest relative focal length found for lenses of roach, *Rutilus rutilus*, is 2.192:1 (Sroczyński, 1977) while in the pike, *Esox lucius*, the equivalent value is 2.383:1 (Sroczyński, 1975a). In the roach alone, the relative focal length for paraxial light rays varied from 2.169 to 2.294:1 in the 30 lenses studied. Thus a universal focal ratio for fish lenses has little meaning. Furthermore, variations in relative focal length reflect inter- and intraspecies variations in lens refractive index gradient.

3.4 SPHERICAL ABERRATION

As mentioned earlier, the amount of spherical aberration exhibited by fish lenses is particularly important because the lens is the only refractive structure of the eye and because of the large-aperture conditions under which it operates. Sroczyński's measures of spherical aberration indicate that although the radially symmetric distribution of refractive index of the fish lens neutralizes most of the spherical aberration that would be manifest in a spherical lens of homogeneous refractive index, some spherical aberration persists. The aberration measured may be positive (undercorrected) or negative (overcorrected). In the first case, paraxial light rays have longer focal lengths than peripheral ones, while in the negative case, paraxial focal lengths are shorter than peripheral ones. In a spherical lens, where shape is not a factor in controlling spherical aberration, positive spherical aberration may be assumed to indicate an insufficient spread in refractive index between centre and periphery while negative spherical aberration suggests that the spread is too great. Typically, the aberration varies non-monotonically between positive and negative spherical aberration within the same lens.

Sroczyński's findings indicate that spherical aberration is corrected to varying degrees in different species, in different populations of the same

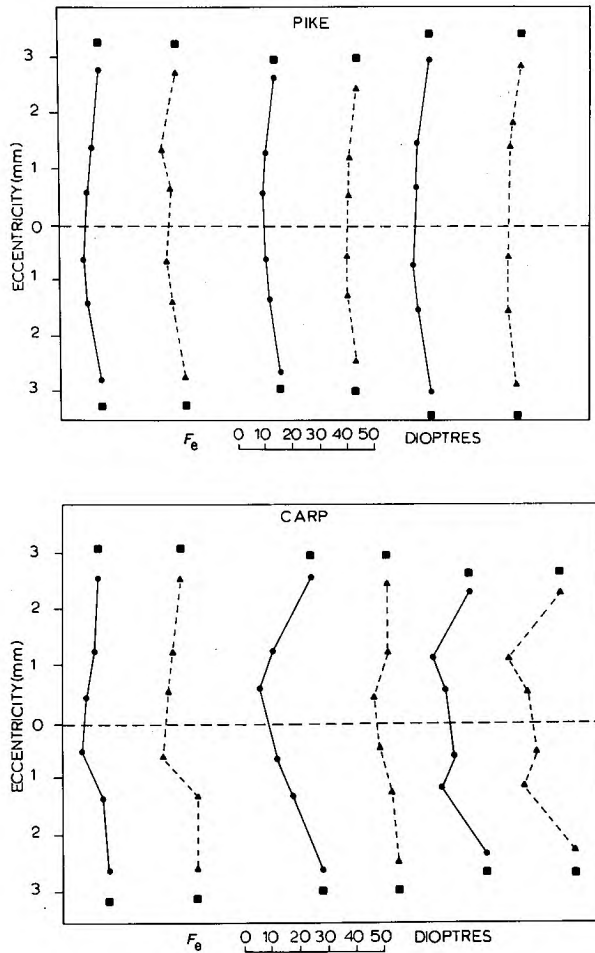


Figure 3.5 Variation in equivalent power (F_e) with incident ray eccentricity from optic axis for (top) pike, *Esox lucius*, and (bottom) carp, *Cyprinus carpio*, lenses. Solid and dashed lines indicate right and left lenses from the same field. Filled squares indicate lens diameter. Curves that are convex to the left indicate positive spherical aberration (reproduced with permission from Kreuzer and Sivak, 1984).

species, and in fish of different age within the same species. For example, spherical aberration of pike lenses from fish with body lengths of 50 cm is less than half that measured from lenses of 30 cm fish (Sroczyński, 1975a). In the European perch, *Perca fluviatilis*, lenses from young fish (body length < 8 cm) show undercorrected spherical aberration while older fish (> 23 cm) have lenses with overcorrected spherical aberration (Sroczyński, 1979a). Lenses

from sexually mature fish are optimally corrected. Considerable differences in quality were found for ruff, *Acerina cernua*, lenses from fish caught in different lakes (Sroczyński, 1981).

Spherical aberration measures of lenses from a number of species of fish, using a photographic method to measure focal length (Sivak, 1982a; Sivak and Kreuzer, 1983; Kreuzer and Sivak, 1984), yield results that are very similar to those of Sroczyński. The method involves the projection of multiple parallel low-power laser beams through lenses maintained in physiological saline. Spherical aberration is determined by measuring focal lengths for pairs of beams of varying eccentricity about the optic axis. The species are chosen to represent a spectrum of visual need as indicated by variations in feeding habits (Sivak, 1973).

In general, spherical aberration is minimized by the developmentally produced variation in lens refractive index. All lenses show some non-monotonic variation in focal length (Sivak and Kreuzer, 1983; Kreuzer and Sivak, 1984). However, the aberration is marked in a non-visual species such as the northern brown bullhead, *Ictalurus nebulosus nebulosus*. Also, the size of the aberration and the between-lens variation in focal length seems to be related to visual need (Figure 3.5). Thus, the lenses from pike, *Esox lucius*, or northern rock bass, *Ambloplites rupestris rupestris*, two sight feeders, show less spherical aberration than those from an omnivorous feeder such as the common carp, *Cyprinus carpio*.

The effect of age was studied by examining lenses from rock bass 2–7 y old. Lens quality, as indicated by a minimal amount of spherical aberration, is optimum in fish 5 y of age. A preliminary examination of lenses from rainbow trout, *Salmo gairdneri*, raised on normal and deficient diets, indicates that nutritional factors need to be considered as well (Kreuzer and Sivak, 1984).

It is of parenthetical interest to note that the lenses of a cephalopod, the short-finned squid, *Illex illecebrosus*, show a significant amount of negative (overcorrected) spherical aberration (Sivak, 1982b). Despite the danger inherent in generalizing from a single species, this finding suggests that cephalopods are not superior to aquatic vertebrates in controlling spherical aberration of the lens.

Fernald and Wright (1983) used the laser-beam approach to measure focal lengths of lenses of the African cichlid, *Haplochromis burtoni* (see Chapter 2). By peeling away the outer layers of the lens and measuring focal lengths of the remaining core, they found that the central core ($0.5\text{--}0.67 \times$ radius) suffers from positive spherical aberration of a nature that indicates that central refractive index has a constant value (1.56). Thus, spherical aberration appears to be minimized only by the refractive index gradient of the cortex of the lens (1.38 at the surface to 1.56 near the core). However, according to Campbell and Sands (1984) these findings can be explained on

the basis of the increasing refractive index difference between the lens surface and the surrounding fluid as layers of the lens are peeled away, coupled with the appearance of positive spherical aberration resulting from the study of a small lens core with a relatively thick laser beam. In fact, ray-tracing analysis of the Fernald and Wright figures confirms the existence of a refractive index gradient throughout the lens (Campbell and Sands, 1984).

3.5 CHROMATIC ABERRATION

Newton (1701, cited by LeGrand, 1967) is credited with first showing that longitudinal chromatic aberration is an important characteristic of the human eye. In fact, experimental measures of human chromatic aberration are greater than theoretical expectation (LeGrand, 1967) because of the exaggerated chromatic dispersion of the crystalline lens, particularly at the short wavelengths of the visible spectrum (Palmer and Sivak, 1981; Sivak and Mandelman, 1982).

Since chromatic dispersion of fish lenses is substantial (Sivak and Mandelman, 1982), it is reasonable to expect significant measures of chromatic aberration to exist. The microscope-optical-bench technique mentioned earlier has been used by a number of authors to measure longitudinal chromatic aberration of the fish lens. With the exception of Pumphrey (1961), who reported very little chromatic aberration in minnow lenses, all authors report substantial amounts.

Expressed as a percentage of some mid-spectrum focal length, chromatic aberrations reported include 2.1% in the guppy, *Lebistes reticulatus* (Eberle, 1968), 4.6% in the rudd, *Scardinius erythrophthalmus* (Scholes, 1975), 4.96% in the rainbow trout, *Salmo gairdneri* (Sroczyński, 1975b), 3.95% in the grey snapper, *Lutjanus griseus*, and 4.04% in the burrfish, *Chilomycterus schoepfi* (Sivak and Bobier, 1978), 4.1% in rock bass, *Ambloplites rupestris rupestris*, and 5.3% in goldfish, *Carassius auratus* (Sivak and Roth, 1978), 4.53% in the perch, *Perca fluviatilis* (Sroczyński, 1979a), 1.8–2.2% in *Haplochromis elegans*, a cichlid (Otten, 1981) and 1.9% in another cichlid, *Haplochromis burtoni* (Fernald and Wright, 1985) (Chapter 2).

Direct comparisons among the results of various authors are difficult because of variations in the spectral limits and/or spectral quality of the targets used. However, efforts to replicate the results of others (e.g. Otten, 1981) indicate that the differences reported are for the most part interspecific. Fernald and Wright (1985) have noted that the aberration is greater in less-visual fish.

The refractive importance of the results of optical-bench experiments has been substantiated by chromoretinoscopic measures of refractive state (Sivak and Bobier, 1978; Sivak and Roth, 1978) and by photographing lens focal

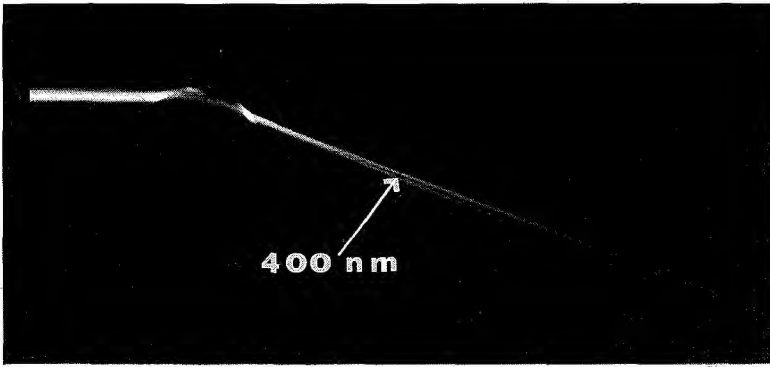


Figure 3.6 Photograph of superimposed helium–neon laser beam ($\lambda = 632 \text{ nm}$) and fluorescing nitrogen laser beam ($\lambda = 400 \text{ nm}$) passing through a rock bass lens. Note two beams spreading apart after refraction by the lens (longitudinal) and chromatic aberration. Lens diameter is approximately 5 mm.

effects on red and blue laser beams (Kreuzer and Sivak, 1985). Chromoretinoscopy involves the measurement of refractive state using a spectrally limited light source. In *L. griseus* and *C. schoepfi*, the refractive difference (470–617 nm) can amount to as much as 8 dioptres. The restricted spectral nature of aquatic habitats, especially those in which the dominant spectral quality is blue or blue-green (Munz and McFarland, 1977), will influence refractive state significantly because of chromatic aberration, as pointed out by Sivak (1974). Therefore it would appear that the colour of the underwater environment is an important factor to consider in the study of the refractive state of the fish eye.

The technique employing red and blue lasers was used to measure longitudinal chromatic aberration of excised crystalline lenses from a spectrum of vertebrates: fish (Figure 3.6), amphibians, birds and mammals (Kreuzer and Sivak, 1985). The aberration (442–632.8 nm) amounts to a relatively constant 4.6% of focal length in all species, although the fish studied show considerable variation. The measured aberration amounts to 4.68% and 4.71% for goldfish, *C. auratus*, and yellow perch, *Perca flavescens*, respectively. However, the aberration measured for rock bass, *A. rupestris*, is much lower (3.15%). The fact that the aberration amounts to only 1.23% when measured for a spherical glass bead emphasizes the dispersive nature of the lens.

Finally, a number of fishes, including *P. flavescens*, possess yellow corneas and lenses (Walls, 1942; Muntz, 1972; Muntz, 1973). Such filters typically act as short-wavelength cut-off filters. Since lens dispersion is greatest for

short wavelengths, chromatic aberration of the lens may be significantly reduced in such species (Chapter 15).

3.6 FUNCTIONAL SIGNIFICANCE OF FISH LENS QUALITY

It was mentioned earlier that fish lens spherical aberration varies considerably among species. Lenses from less-visual fish, such as the northern brown bullhead and the carp, show more variation in focal length than lenses from visual feeders (Kreuzer and Sivak, 1984). Also, chromatic aberration appears to be greater in lenses from less-visual fish (Fernald and Wright, 1985). These findings suggest that there exists selective pressure for superior lens quality where such quality confers an advantage.

Fernald and Wright (1985), however, argue that because the resolving power of the fish lens (of *H. burtoni*) is considerably greater ($10\times$) than the resolving power of the retina, as indicated by the spacing of the cone receptors, lens quality can never limit visual acuity.

While retinal photoreceptor separation is a common method used to calculate ocular acuity limits (e.g. Hairston *et al.*, 1982), this approach has a number of limitations, the principal one being that retinal receptors are never synaptically associated with direct neuronal pathways to higher levels in the central nervous system. Rather, retinal synaptic anatomy, both at the outer and inner plexiform layers, is such that receptor communications include widespread lateral interconnections (Hogan *et al.*, 1971). Retinal output, as indicated by the electrophysiological responses (receptive fields) of ganglion-cell axons, is completely removed from the dimension used in describing the widths of retinal cones. This point is not intended as a denial of the fact that receptor size and receptor density is an important relative measure of retinal acuity limits. The variation of receptor anatomy of the human retina in the area of the fovea as compared to more peripheral regions is but one obvious example. Nevertheless, efforts to show that absolute anatomical measurement agrees with measures of acuity should be questioned, and successful comparisons may be fortuitous.

A second limitation of the photoreceptor size and separation approach is the fact that visual acuity is not a well defined concept and visual behaviour may be related to one or more acuity measures at any given time. Westheimer (1987), for example, refers to three main acuity criteria: minimum visible, minimum resolvable and minimum discriminable (hyperacuity). Measures of human minimum resolvable acuity, i.e. the minimum separation required for the human eye to resolve two points or two lines, yields magnitudes (30 seconds of arc to 1 minute of arc) which are comparable to receptor anatomy. However, measures of the minimum visible acuity and tasks involving hyperacuity (e.g. vernier acuity) are an order of magnitude smaller (1–3 s). Such acuities obviously cannot be related to receptor dimensions and

separations, at least not directly. Fernald and Wright (1985) suggest that acuity is lost as visual information is transmitted to higher-order neural centres. In fact, loss of visual information at higher levels is unlikely (Westheimer, 1987). Geisler and Hamilton (1986) point out that two-dimensional sampling theory may be used to explain how various receptive field shapes and patterns may be used to show how retinal image information is preserved at higher levels in the visual pathways, despite the fact that the information provided by post-receptor cells consists of large overlapping receptive fields rather than the small non-overlapping retinal locations appropriate for individual receptors.

The foregoing suggests that fish lens optical quality may be important to visual behaviour. Snyder *et al.* (1986) point out that increasing the resolving capacity of the lens above that of the receptor mosaic improves the contrast sensitivity of an animal's visual system, although this is achieved at the expense of 'aliasing' (misinterpretation of patterns with frequencies higher than the retina's 'maximum resolvable' frequency). The extreme 'mismatch' between the resolving power of the lens and retina in fish may be an adaptation to the low-contrast underwater environment (Wetterer, unpublished; Chapter 11).

3.7 CONCLUDING REMARKS

The preceding review indicates that the fish lens is not the optical standard suggested by such authors as Walls (1942). Rather, as the fish lens is subjected to greater scrutiny, wide interspecific variations in such measures as shape, relative focal length, spherical aberration and chromatic aberration indicate that a single universal model is inappropriate. Scroczyński (1977) writes that '... investigations on the spherical aberration in fish, instead of bringing some clarity to a problem of the functional efficiency of crystalline lens, lead to a statement of many other questions. . . .'

Given the large numbers of fishes (25 000 species out of a total of about 50 000 vertebrates: Walter and Sayles, 1959) and wide variations in life habits, some difference in lens quality performance may be expected. The major point is that generalizations based on experimental evidence limited to small numbers of species can lead to the development of overly restrictive models of the visual apparatus. As Hughes (1977) writes, 'The situation is improving but much "bread-and-butter" work remains. . . .'

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