Chapter 2

The optical system of fishes

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2.1 INTRODUCTION

How fish see has probably puzzled anyone who has ever opened their eyes underwater whilst swimming to discover a shimmering unfocused world. It has certainly intrigued both scientists and fishermen, because fish appear to see quite well indeed. The eyes of fishes, like those of other more familiar animals, have evolved adaptations responsible for two main visual functions: (1) to collect light, and (2) to form a focused image for analysis by the retina. In fish, the additional challenge of seeing underwater has resulted in novel solutions to these fundamental problems. This chapter will discuss two major features of fish visual systems: **optics**, which is the collection of light and formation of an image by the lens, and **accommodation**, which is the focusing of images on the retina.

2.2 OPTICS

Since eyes must obey fundamental physical laws, constraints on their optics and overall structure offer a straightforward problem. Nonetheless, some of the details of just how the optics of the fish eye work have been assessed in only a handful of species, and then only to a limited extent. However, the general principles now seem clear, and the selective advantages accruing to fish with particular refinements to these principles can be assayed.

Collection of light

Both the sensitivity and the acuity of an eye depend on the brightness of the image reaching the retina. In viewing a point source of intensity I (in candelas), in which all the light entering the eye comes from a single point,

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the flux F (in lumens) in the eye is given by:

$$F = (I\ P_a)\ /\ D^2 \tag{2.1}$$

where P_a is pupillary area and D is distance from the source to the plane of the pupil (Fernald, 1988). Thus the brightness of the image increases in proportion to both the intensity of the source and the area of the pupil, and decreases in proportion to the square of the distance from the source to the plane of the pupil. In the deep sea, there may well exist point sources of light, such as bioluminescent organisms or light-emitting organs of fish, so light-gathering ability was probably a selective force leading to the large eyes of deep-sea fish. However, fish living in higher levels of ambient daytime light near the surface of the water view scenes illuminated by extended sources for which the retinal illuminance E (in lumens m^{-1}) is:

$$E = (L\ P_a)\ /\ f^2 \tag{2.2}$$

where L is luminance of the extended surface source, P_a is pupillary area, and f is focal length (Fernald, 1988). How does the light intensity on the retina change with eye size when scenes illuminated by extended sources are viewed?

In fish, the focal length divided by the lens radius (r) is termed **Matthiessen's ratio** (Matthiessen, 1882) (Table 2.1), which is constant within any given species:

$$m = f\ /\ r \tag{2.3}$$

and the effective aperture diameter is the lens diameter, since the iris does not cover any part of the lens (Fernald and Wright, 1985a).

Because of these two relationships, the retinal illuminance can be related to the well-known f-number of a lens, which is:

$$\text{f-number} = \text{focal length} \ /\ \text{aperture diameter} = \frac{f}{d} = \frac{f}{2r} \tag{2.4}$$

Therefore, for fish:

$$\text{f-number} = \frac{f}{2r} = \frac{m\,r}{2r} = \frac{m}{2} \tag{2.5}$$

where m is Matthiessen's ratio.

Since the pupillary area equals πr^2, where r is lens radius, the retinal illuminance can be expressed in terms of f-number by combining Equations 2.2 and 2.5:

$$E = (\pi\ /\ 4)\ L\ (1\ /\ \text{f-number})^2 \tag{2.6}$$