Chapter 18

Aquatic Adaptations in Fish Eyes

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> To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree.
>
> (Charles Darwin, *The Origin of Species*, 1859, p. 168)

Of all the sense organs, eyes have probably attracted the most attention because of both their central importance and intricate construction. Darwin knew that such "organs of extreme perfection and complication" posed a crucial test of his theory because they seemed *too* good to have been shaped by natural selection (Darwin [1859] 1958). Since eyes must obey the optical laws of physics, fundamental physical constraints on their structure provide an important analytical basis for understanding adaptive ocular specializations. In light of these physical constraints, inferences about the selective forces that have shaped eye design can be made with some confidence, particularly in the study of aquatic eyes.

Fish eyes offer an unusually interesting and accessible opportunity to ask general questions about visual evolution, development, and function (Fernald 1984). Although a great deal of work has been done on the domestic goldfish, this narrow experimental focus obscures the fact that bony fish form the largest class of vertebrates, comprising over 25,000 species. Evidence of their success can be found in the adaptive radiation of forms occupying an extraordinary range of habitats. Fish eyes and brains variously reflect success in mastering different life history strategies with the unsurprising general rule that the favored sensory modality occupies disproportionately more brain volume (see Geiger 1956).

There are several summaries of information about the fish eye available, so here I will present primarily recent findings. Since fish eyes have a relatively standard construction, with some deviations resulting from adaptations to specialized situations, I will first discuss underlying physical constraints that apply generally to the evolution of eyes. Then I will analyze various structures that have evolved to meet these constraints in teleost fish and, finally, present some new evidence about novel solutions to problems posed by regulation of fish eye growth.

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Physical Constraints on Eye Design

In striking contrast to the enormous variety of eye types that have evolved among invertebrate species (Land 1981; see also Chap. 16), there exists essentially a single type of image-forming vertebrate eye. Because the vertebrate eye first evolved in water it is sensitive to only a narrow band of wavelengths of electromagnetic radiation, which are transmitted through water without significant attenuation (Fig. 18.1). The only other band with comparably low transmitted attenuation ($< 10^3$ Hz) has been exploited by weakly electric fish (see Chaps. 9 and 33). At low frequencies, however, the very long wavelengths make image formation impossible, since any detector must be large relative to the wavelengths detected. As a consequence, electric fish have detectors distributed all along their bodies from whose response they "compute" an image.

The exploitation of light for vision has proven a powerful selective force in all organisms (see Chap. 3). Light travels in straight lines, can be reflected, and varies in both wavelength (color) and intensity. Many of the design principles and even apparent errors we recognize in eyes reflect constraints arising directly from the physical properties of light. Natural selection cannot be expected to produce an error-free eye, but rather one just good enough for the animal's particular circumstances (Darwin 1859, 187). To inform their owners about the visual world, image-forming eyes must both *capture light* and *resolve it into images*. These two requirements for vision have shaped the evolution of eyes throughout the animal kingdom.

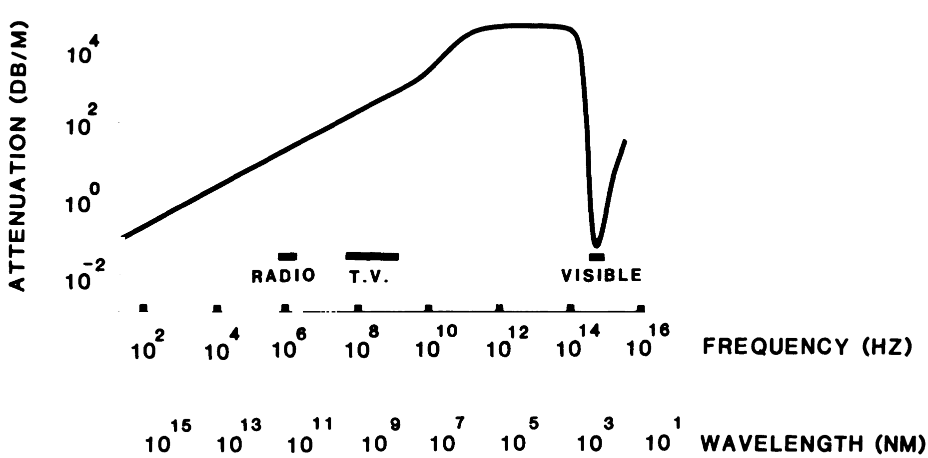

Figure 18.1. The attenuation (dB/m) of electromagnetic radiation in seawater plotted as a function of frequency (Hz) and wavelength (nm) of that radiation. Bands of electromagnetic energy used for radio and television transmission are shown, as is the narrow band corresponding to visible light.