4 ROLE OF VISION IN FISH BEHAVIOUR

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Despite the generally poor quality of underwater images, fish depend a great deal on vision as a source of sensory information. All but a few (mainly cave-dwelling species) have well-developed eyes, and in those forms that inhabit clear-water environments, the variety of colour patterns and specific movements that they display invites comparison between them and the most visually oriented species among birds and mammals. Because of the physical nature of light and its complex interactions with the environment, a variety of different properties of visible objects can be recognised, differing either in type (i.e. brightness, hue, texture, contour, etc.), or degree (such as patch size or pattern grain). Comparative properties such as colour contrast or brightness contrast can also be identified. The extent to which particular visual properties are important depends on (a) the type of visually mediated behaviour, and (b) the restrictions to visual signalling imposed by the aquatic medium.

Visually mediated behaviour ranges in complexity from the simple alerting or attentive state evoked by any novel but non-specific visual event, to the triggering of an elaborate fixed action pattern by means of a highly specific visual signal which consists of a precise grouping of visual properties. The structure of the visual signal enables it to remain effective even when a high concentration of suspended matter in the water alters the perceived properties of hue and texture. At the same time, the more complex signals must require more specialised processing by the nervous system and longer reaction times. It is perhaps slightly ironic that most of the waters of very high optical purity inhabited by fishes are so lacking in nutrients that they support only a meagre fauna. Wastwater in Cumbria is perhaps an example of such a water in the UK.

The Optical Properties of Natural Waters and their Effects on Underwater Visibility

(1) Generalised Habitats

In a few oceanic waters and a number of dystrophic lakes there is very little suspended matter. Solar radiation can penetrate to considerable depths (below 100 m) but ultraviolet and long wavelengths are attenuated by the water molecules, resulting in maximum transmission being between 400 and 500 nm. In consequence these waters have a bluish appearance.

Most waters contain appreciable quantities of mineral and organic matter (especially chlorophyll), which absorbs most of the light at depths of

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25 m or so and narrows and shifts the spectral composition to a band between 500 and 600 nm, giving a greenish or yellowish cast to the water. A majority of coastal waters, lowland (oligotrophic and eutrophic) ponds, and rivers fall into this category. Less common are those waters, mainly fresh, carrying high concentrations of silt, or plant breakdown products which give them a brownish or reddish appearance. Here little light penetrates below 3 m, and this is mostly at wavelengths above 600 nm. The so-called 'black' (Muntz 1973) or 'infra-red' (Levine, Lobel and MacNichol 1980) waters are typified by some of the tropical fresh waters in South America. These are heavily stained but transparent rivers, usually of high acidity, and are contrasted with uncoloured 'white' waters, which may form part of the same river system, as in the case of the Rio Negro. Heavily peat-stained tarns in Northern Britain (e.g. Wise Een Tarn, Cumbria) provide a somewhat similar example. Opaque reddish waters are found where red clays form part of the watershed (Pahang and Kalang Rivers, Malaysia). Clearly, fish living in waters that approximate to these types operate under special visual conditions.

(2) Lines of Sight (see Figure 4.1)

As Levine *et al.* (1980) have pointed out, the amount and spectral quality of light entering a fish's eye will differ according to the line of sight involved. The overhead view will involve the shortest optical path length and thus luminance attenuation and spectral shift will be least. Further, objects overhead above the water surface, within a solid angle of 97°, can be viewed (Snell's window). Horizontal lines of sight will be subject to lower light levels and greater spectral shifts due to the longer optical path involved. Objects viewed in this direction will have their apparent contrast reduced by veiling light scattered from particles between eye and object. Further, as the object recedes from the eye, the effect of the veiling light becomes greater, the spectral reflectance of the object is increasingly shifted towards that of the dominant spacelight, and object brightness approximates to background. The downward line of sight from the eye involves the longest optical pathway, with the greatest effects on both the brightness and spectral properties of objects viewed. In shallow water, most of the visual background is provided by the bottom of the pond or river.

(3) Temporal and Spatial Changes in Underwater Visibility in Natural Waters

Stratification in optical properties is perhaps most noticeable in fresh waters where a seasonal cycle occurs. The most well known of these changes involves the warm-water layer that forms in lakes and ponds as sunlight hours increase in spring and early summer. The separation of a lighter surface layer (the epilimnion) due to the action of the sun produces a boundary layer across which the temperature changes abruptly. In large lakes the zone of greatest change (thermocline) occurs between 5 m and