

8 Retinal Sampling and the Visual Field in Fishes

Shaun P. Collin and Julia Shand

Abstract

The retina of aquatic vertebrates comprises a complex array of sampling elements, each subtending a specific region of the visual field. The transformation of light energy (an optical image) into electrical energy (a neural image) across the retina is nonuniform and reflects the complexity and diversity of the visual field. The identification of localized differences in the function, arrangement, and distribution of retinal neurons in fishes has revealed a level of plasticity unparalleled in vertebrates. Specialized retinal regions (areae centrales, horizontal streaks, and foveae) are examined with respect to both photoreceptor and ganglion cell sampling and the optimization of spatial resolving power and sensitivity. Selective sampling of the binocular visual field, specific asymmetries in the sampling of the dorsal and ventral hemifields, and the number of specializations that comprise only subpopulations of neurons also indicate that the mechanisms controlling the spacing, density, and regularity of retinal neurons are highly complex. Both photoreceptor and ganglion cell arrays change during development, and are affected by changes in the spectral composition, intensity, and symmetry of the photic environment. These arrays typically alter during a transition from one feeding strategy to another. The location of specialized retinal regions subtending the binocular visual field can even alter during development due to the continual growth of the retina throughout life and a changing visual environment.

1. Introduction

Bony and cartilaginous fishes occupy a large diversity of natural environments including the light-limited deep-sea, the turbid water of estuaries and rivers, and brightly lit coral reefs. Their activity patterns also vary according to

the ambient light levels, where many species are characterized as diurnal, crepuscular, or nocturnal, although many may cross these behavioral boundaries. The eyes of these aquatic vertebrates must therefore provide an accurate representation of the visual world within an enormous number of photic environments. The

large directional differences in intensity and spectral composition of the underwater light, the amount of particulate matter suspended in the water, turbidity, and the need to find food, predator, and mate have all been the driving forces in the evolution of a diverse range of retinal specializations. Although most aquatic animals are active during the day, many are crepuscular or even nocturnal with some species changing their diurnal activity and habitat during development. In all cases, the photic environment differs, which places selective pressure on the eye and its ability to effectively sample its visual field. Although the various components of the ocular media (cornea, lens, and vitreous) may be adapted to differentially filter different parts of the electromagnetic spectrum, it is the retina that ultimately samples the visual environment, transforming light energy or an "optical image" into electrical energy or a "neural image." The process of transduction is performed by the photoreceptors, which line the back of the retina, with each receptor subtending a minute part of the visual field. The transfer of information to the visual centers of the brain is mediated via a series of interneurons. Signals reaching the output (ganglion) cells, lining the inside of the retina, are carried to the central nervous system via ganglion cell axons, which comprise the optic nerve. Every point in each species' visual field is subtended by a corresponding point on the neural retina, which, in turn, is retinotopically mapped onto the optic tectum.

The distribution of both photoreceptors and ganglion cells across the retina is known to be nonuniform in many aquatic vertebrates, and topographic analyses have recently become a powerful tool in predicting the importance each species places on observing objects in specific regions of their visual field (Collin and Pettigrew, 1988a,b; Collin, 1999; Bozzano and Collin, 2000; Shand et al., 2000a). Localized increases in retinal cell density determine the spatial resolving power of the eye, where the distribution of retinal neurons in each species is unique and closely reflects each species' perceived world (Collin and Pettigrew, 1988a,b; 1989). Optical constraints such as the size of the eye,

the size and shape of the pupil, the location of the eyes in the head, the degree of eye movement, the size of the visual field, and the degree of binocular overlap all contribute to the optimal placement of retinal regions for increased sampling (Fig. 8.1; see color plate). This chapter reviews the adaptive strategies employed by a range of cartilaginous and bony fishes from various lifestyles and habitats. These are examined with respect to the optimization of retinal sampling of an image in specific regions of the visual field. These retinal specializations will also be discussed in the context of changes in both the photic environment and the visual field during development and growth and the magnification of these specialized zones within the central nervous system.

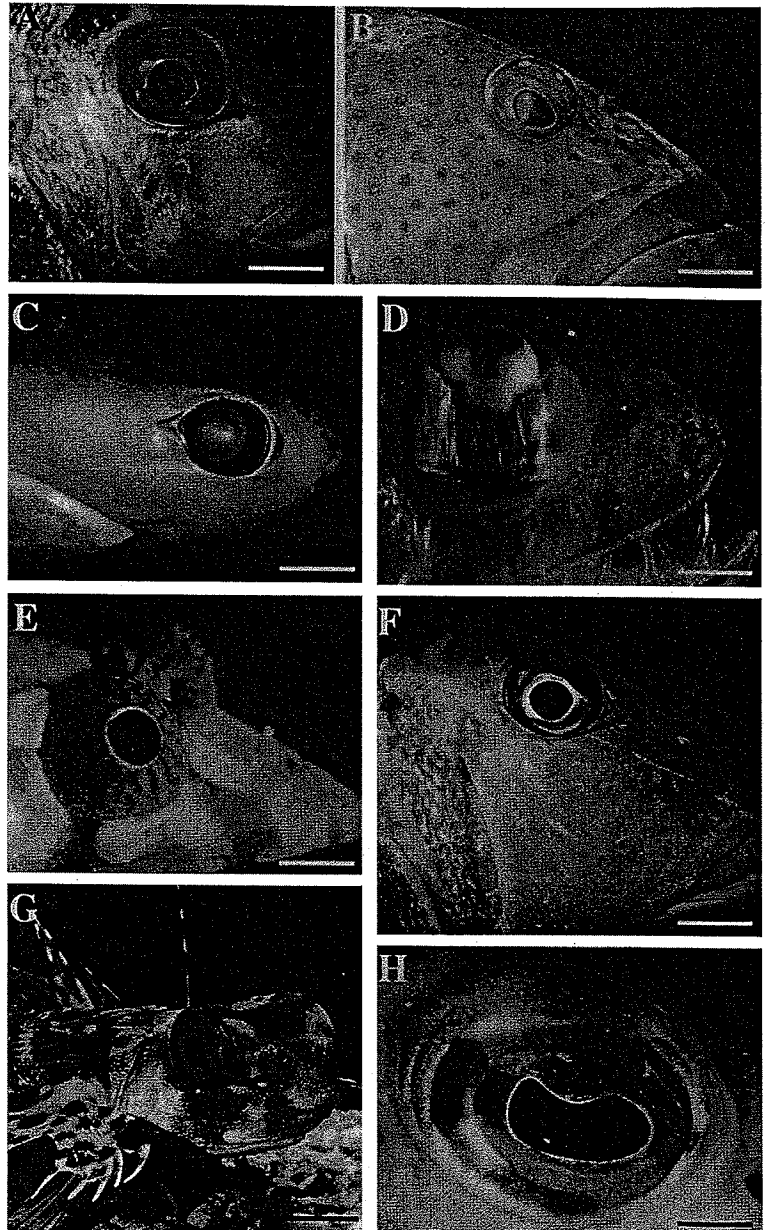
2. The Retinal Elements of Visual Sampling

2.1. Photoreceptors

The photoreceptor array in fishes may be comprised of single, unequal double, equal double, triple, or even quadruple cones and rods, which are most commonly aligned as a single layer of receptors along the outer limiting membrane (OLM). However, possibly due to the need to reduce chromatic aberration produced by the lens, some subpopulations of receptors migrate out of this monolayer, with the short wavelength-sensitive photoreceptors lying in a more vitreal position than long-wavelength receptors (Eberle, 1967; Scholes, 1975; Shand, 1994). Photoreceptor types also undergo retinomotor movements in response to changing levels of light intensity and therefore may be arranged in staggered rows. Multiple rows or banks of photoreceptors (rods) occur in many deep-sea teleosts where, in some species, up to 28 banks of rods may form a fovea externa (see below). This is done in an effort to increase sensitivity (Locket, 1985; Fröhlich and Wagner, 1998) and provides the potential to mediate color vision (Denton and Locket, 1989).

The area of the visual environment sampled by a single photoreceptor may differ among

FIGURE 8.1. Diversity of eye size and shape in bony and cartilaginous fishes. (A) The collared sea bream *Gymnocranius bitorquatus* showing a binocular sighting groove etched into the snout. (B) The coral trout *Plectropoma leopardus* showing a colored corneal reflex and a rostrally tapered pupil. (C) The cookie-cutter shark *Isistius brasiliensis* with large eyes and a blue tapetal reflex. (D) The deep-sea pearleye *Scopelarchus michael-sarsi* with its tubular eyes and large spherical lens. (Photograph kindly provided by N.J. Marshall.) (E) The sandlance *Limnichthyes fasciatus* showing its dorsal, protruding eyes. (F) The sweetlip, *Lethrinus chrysotomus* showing its binocular sighting groove. (G) The oriental sea robin *Dactyloptena orientalis* perched on its modified pectoral fins and showing its highly positioned eyes. (H) A close up of the eye of the weever fish *Parapercis cylindrica* showing its crescent-shaped pupil. Scale bars, 10mm (A, B); 20mm (C); 2mm (D); 0.5mm (E); 15mm (F); 10mm (G); 1mm (H). (See color plate)



species and appears to be governed by the visual demands of the animal. Increased spatial resolving power is mediated by tightly packed arrays of small photoreceptors. However, the minimum diameter for a receptor outer segment, even in a small eye, is approximately $1\mu\text{m}$. Below this diameter, the photoreceptors fail to act as waveguides and light propagates both inside and outside the receptor, causing

“optical crosstalk” and degradation of the neural signal (Kirschfeld, 1976; Land, 1981). At the other end of the scale, some photoreceptor outer segments reach $8\mu\text{m}$ in diameter, specializing in maximizing photon capture to increase sensitivity. Teleosts inhabiting low-light conditions are also known to compromise resolution by grouping their photoreceptors into bundles, effectively sampling the visual field with large

macroreceptors each comprised of up to 50 sampling elements (e.g., in the pearleye, *Scopelarchus michaelisarsi*, Collin et al., 1998 and the goldeye, *Hiodon alosoides*, Braekevelt, 1982).

A range of intracellular inclusions characterize many photoreceptors both morphologically and spectrally. Aggregations of glycogen located within the inner segment constitute a paraboloid in various species of primitive ray-finned fishes including the Florida garfish *Lepisosteus platyrhynchus* (Collin and Collin, 1993) and the bowfin *Amia calva* (Munk, 1968). These myoidal inclusions are thought to act as an energy store. Although rare in euteleosts, oil droplets have been described in various species of primitive fishes including the coelacanth (Walls, 1942), the Australian lungfish (Robinson, 1994), and some species of sturgeon (Munk, 1968; Govardovskii et al., 1992). As in reptiles (Ohtsuka, 1985; Kolb and Jones, 1987), birds (Bowmaker and Martin, 1985; Partridge, 1989; Hart et al., 1998), and nonplacental mammals (O'Day, 1938; Braekevelt, 1973; Arrese et al., 2002), the different types of oil droplets in these fishes (colored and colorless) are thought to either act as cutoff filters, especially for short wavelengths, or aid in focusing light onto the outer segments (Pedler and Tilly, 1964; Young and Martin, 1984; Wong, 1989). A similar function has been attributed to the large ellipsoidal inclusions (ellipsosomes) within the inner segment of cones in a small group of cyprinids (Borwein and Hollenberg, 1973; Anctil and Ali, 1976; MacNichol et al., 1978; Nag and Bhattacharjee, 1989, 1995; Nag, 1995; Novales-Flamarique and Hárosi, 2000). Described by Franz (1932) as false-oil droplets, these large globules, formed from mitochondria, contain a dense heme pigment (Avery and Bowmaker, 1982), are shortwave-absorbing cutoff filters, and tune the incoming light before it strikes the outer segment. The recent finding of ellipsosomes in lampreys (Collin et al., 1999; Collin and Potter, 2000) suggests that these inclusions may be the precursors to (gnathostomatous) vertebrate oil droplets.

Once light enters each photoreceptor cell, it is ultimately the visual pigments within the outer segment that initiate the process of visual

transduction by the absorption of light in specific regions of the electromagnetic spectrum. Diurnal shallow-living fishes are known to possess up to four different cones types, providing sensitivity across the spectrum from ultraviolet (short wavelengths) to infrared (long wavelengths). Those living in turbid and low-light conditions, along with crepuscular species, tend to possess only two cone types. However, in most species thus far investigated, the spectral absorption of the long wavelength-sensitive double cones can be related to the spectral qualities of the body of water in which the fishes are found (see reviews by Lythgoe, 1984; Lythgoe and Partridge, 1989; Bowmaker, 1995; Partridge and Cummings, 1999; Chapter 17). The absorption of the single cones is offset to shorter wavelengths (blue and/or UV sensitive) than the ambient light and is thought to facilitate detection of contrast against the prevailing background light (Lythgoe and Partridge, 1991). The rod photoreceptors are predominantly sensitive to medium wavelengths (approximately 500 nm) and show little variation in spectral sensitivity, with the exception of deep-sea fishes, which mainly absorb shorter-wavelength light than their shallow-living relatives and are thought to be "tuned" to increase sensitivity and detect prey that use bioluminescence to camouflage their silhouettes against the downwelling light (Douglas et al., 1998b). The structure of visual pigments and the mechanisms by which they are spectrally tuned is discussed below (see Sections 4.2 and 5.3) and in Chapter 17.

2.2. Retinal Interneurons

In the vertebrate retina, light energy is transformed into graded potentials at the level of the photoreceptor cells and conveyed, via interneurons such as bipolar, horizontal, and amacrine cells, to the third-order neurons (ganglion cells) before being transmitted as impulses to the brain via the optic nerve. The bipolar cells transmit signals directly from the photoreceptors to the ganglion cells and a diverse range of cell shapes and sizes have been identified (about 10 different subtypes according to Naka and Carraway, 1975 and Scholes, 1975). Hori-

zontal cells transfer information laterally across the retina and are capable of mediating chromatic interactions between different spectral cone types, generating the antagonistic surround of the bipolar cell receptive field and modulating spatial summation (Wagner, 1990). There is a large diversity of amacrine cell types in teleosts and the characterization of the range of cell types is beyond the scope of this chapter.

2.3. Ganglion Cells

Retinal ganglion cells are third-order neurons lining the inner retina that possess an axon that transmits the retinal output to the visual centers of the brain via the optic nerve. Ganglion cells predominantly lie within the ganglion cell layer but specific populations are also located within the inner plexiform and inner nuclear layers (Collin and Northcutt, 1993). The axons of ganglion cells are predominantly unmyelinated within the retina but become myelinated within the optic nerve. Ganglion cells receive input from bipolar and amacrine cells via both ribbon and chemical synapses, respectively, although Sakai et al. (1986) have established that the distal dendrites of some ganglion cells also possess presynaptic terminals to bipolar, amacrine, and other ganglion cell processes. The finding suggests that ganglion cells may be able to establish direct interactions with other ganglion cells and that they are able to shape their own response properties through microcircuits formed by their presynaptic dendrites (Sakai et al., 1986).

Various ganglion cell types have been identified in teleosts (Ito and Murakami, 1984; Hitchcock and Easter, 1986; Collin, 1989) and up to 11 different morphological types have been identified in the channel catfish, *Ictalurus punctatus* (Naka and Carraway, 1975; Dunn-Meynell and Sharma, 1986). Morphologically, the dendritic field size, stratification, and central projections are required for characterization, although all three criteria have not been analyzed concurrently in a single species of teleost. As in the human fovea, it is thought that subtypes of ganglion cells mediate high spatial resolving power and are located within defined

retinal regions. In the coral trout *Plectropoma leopardus*, small Class 1 cells with a soma size of up to $16.8\mu\text{m}^2$ and a fan-shaped dendritic arbor are the only ganglion cell type to be found within the temporo-ventral area centralis (Collin, 1989).

Retrograde labeling from the optic nerve is necessary for definitive identification of the retinal ganglion cell population. However, analyses of the distribution and peak density of all neurons located within the ganglion cell layer closely mirrors that of retrogradely labeled ganglion cells, despite the inclusion of amacrine cells known to be present in the ganglion cell layer of fishes (Collin and Pettigrew, 1988c; Shand et al., 2000b). However, the proportions of ganglion to displaced amacrine cells can vary between species. The axons of the optic fiber layer about the inner limiting membrane and traverse the retina as a continuous sheet or as fascicular bundles (Collin and Northcutt, 1993; Douglas et al., 2002). In lampreys, where a significant proportion of the retinal ganglion cells (75%) lie within the inner nuclear layer, axons exit the retina from the inner nuclear and inner plexiform layer boundary (Fritzsche and Collin, 1990).

As fish grow, new retinal cells, including ganglion cells, are continually being added to the retinal periphery throughout life (Johns, 1977). The new ganglion cells form annuli and, as new retinal tissue is added, subtend continually changing regions of the visual field as each cohort of cells becomes located more centrally. Since the visual world is retinotopically mapped onto the optic tectum, the synapses formed by the ganglion cell axons must also be continually changing.

3. The Visual Field in Fishes

3.1. Eye Position and the Visual Field

The size and shape of the visual field is crucial for the detection of mates, predators, and prey and, in conjunction with eye mobility, govern the development and location of retinal specializations. Despite the growing number of studies investigating the range of retinal sam-

pling strategies in fishes, very few have concomitantly measured the extent of the visual field. Visual field size is species-specific and varies according to the position of the eyes within the head, the shape of the cranium, the depth of the eye socket, and eye mobility (Fig. 8.1). However, the visual field of most laterally placed eyes, when stationary, is also governed by the shape of the scleral eyecup, the extent to which the eye protrudes from the body contour,

the distance of accommodatory lens movement, and the shape of the pupil. In most fishes, the pupil is not moveable, although some benthic species use pupillary movement for camouflage (Douglas et al., 1998a, 2002). In the Florida garfish, *Lepisosteus platyrhynchus*, which possesses laterally placed eyes, the monocular visual field is approximately 137° in the horizontal plane (Collin and Northcutt, 1995; Fig. 8.2), while in the gurnard, *Trigla*

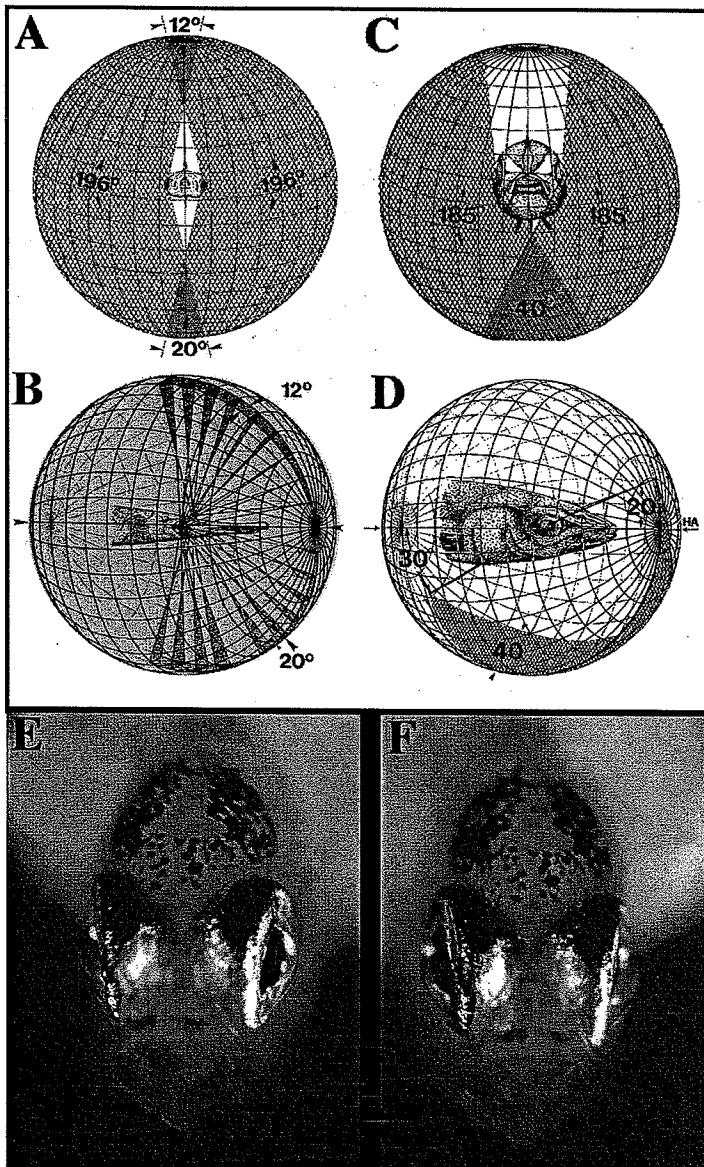


FIGURE 8.2. Visual fields in bony fishes. (A, B) The monocular visual field of the two eyes in the Florida garfish *Lepisosteus platyrhynchus* measured ophthalmoscopically shown from the front (A) and from the side (B). Note the small degree of binocular overlap in the dorsal and ventral fields. (Adapted from Collin and Northcutt, 1993.) (C, D) The monocular visual field of the two eyes in the deep-sea smoothhead *Conocara macroptera* from the front (C) and from the side (D) showing the large degree of binocular overlap in the ventral visual field. (S.P. Collin and, D.L. Lloyd, unpublished.) (E, F) Stereo pair of the head of the black bream *Acanthopagrus butcheri*. When these two images are fused, the part of the visual field subtended by both eyes can be better appreciated. HA, horizontal axis.

corax, the monocular visual field extends over 170° (Kahmann, 1934).

Although the refractive index of the cornea and the surrounding water effectively negate any refraction at the corneal interface in aquatic vertebrates, the radius of curvature of the cornea also determines the size of the visual field in a number of unusual fishes. The position of the eyes in the head and the ability to maintain the head so that the dorsal region of the eyes is partially exposed to the air governs the extent of the visual field in the four-eyed fish *Anableps anableps* (Sivak, 1976). Gliding just beneath the surface of the water, this species enjoys both aerial and aquatic visual fields simultaneously by possessing a lens (and overlying cornea) with different radii of curvature along the two axes. The unique cornea of the sandlance *Limnichthyes fasciatus* possesses a corneal lenticle with a refractive power of 200 dioptres (in water) and a radius of curvature of 0.24 mm (Pettigrew and Collin, 1995; Pettigrew et al., 2000). This compares to a radius of curvature of 3.2 mm for the nonrefractive cornea in the salamanderfish *Lepidogalaxias salamandroides* (Collin and Collin, 1988a, 1996). Combined with a flattened lens with a power of 550 dioptres, the small radius of curvature of the cornea in *L. fasciatus* increases the visual field. However, the independent and highly mobile eyes of this species extend its visual field to 180° horizontally and 90° vertically (Fritsches and Marshall, 1999) providing a substantial area of binocular overlap (Fig. 8.1E).

Ocular adaptations to increase the binocular field include a rostral tapering of the pupil leaving an aphakic gap that allows more light to strike the (temporal) retina, a binocular sighting groove etched into the snout (Fig. 8.1A,B,F), conjugated frontal eye rotation, and an invagination of the iris, for example, in some species of deep-sea fishes with tubular eyes (Collin et al., 1997; Fig. 8.1D). In the gurnard, *Triglia corax*, the binocular overlap is low (8°) while in various predatory serranids (*Plectropoma leopardus* 36°, *Serranus scriba* 40°, *Epinephalus fasciatus* 54°) the binocular overlap is high (Kahmann, 1934; S.P. Collin and J.D. Pettigrew, unpublished). These species all possess a temporal area centralis and accu-

rately align the retinal specialization upon prey objects by conjugated saccadic eye movements before striking. In the Florida garfish *Lepisosteus platyrhincus*, a large (vertical) monocular field of 196° gives rise to a binocular overlap of 12° (dorsal) and 20° (ventral) (Fig. 8.2A,B). The deep-sea smoothheads *Conocara* sp. possess a ventral binocular overlap of 40° (Fig. 8.2C,D) while the eyes of the larval black bream *Acanthopagrus butcheri* subtend a binocular overlap of 21° in the frontal visual field (Fig. 8.2E,F).

3.1. Eye Movements and the Visual Field

Although the extent of the visual field does not alter during eye movement, the degree of binocular overlap changes during ocular fixation. Governed structurally by both the development of the extraocular eye muscles and the relative size of the eye and its supporting socket, the degree of eye mobility in fishes is also closely related to habitat and visual demands. Most species possess some eye mobility but the extent may be masked to the observer by the movement of the globe beneath a secondary spectacle (or scleral cornea), which offers protection or streamlines the contour of the eye (Collin and Collin, 2001). Although head movements are relatively rare in fishes, when this presents a predatory threat (e.g., in the salamanderfish *Lepidogalaxias salamandroides*), a structural modification of the vertebrae actually enables this species to flex its "neck" in order to scan its visual field without any apparent eye movement (Berra and Allen, 1989; Collin and Collin, 1996).

Eye movements, independent of head or body movements, are likely to have evolved to stabilize the image of the visual world on the retina. Fast eye shifts or saccades, smooth pursuit movements that follow moving objects, and vergence, which adjusts the eyes for different viewing distances, are correlated with the development of retinal specializations such as a fovea or area centralis (Walls, 1942) (see below). A range of eye movements has been characterized in fishes by Fritsches and Marshall (2002). These include conjugate (moving the eyes in the same direction),

vergent (moving the eyes in opposite directions), and independent eye movements. Fritsches and Marshall (2002) analyzed the optomotor range of three foveate teleosts and found that the position of the fovea was correlated with dynamic eye movement. The sand-lance *Limnichthyes fasciatus* can strike at prey within a strike zone of 130° using its centrally located fovea without any changes in body position. In contrast, the pipefish *Corythoichthyes* sp. and sandperch *Parapercis cylindrica*, possess asynchronous eye movements and both use body movements to orient their temporal foveae toward prey (Collin and Collin, 1999; Fritsches and Marshall, 2002).

Various species of fishes have evolved mechanisms to inhibit "retinal slip" during swimming and elicit compensatory eye movements in response to changes in orientation and the visual scene. This is achieved by fast gaze shifts (saccades), which render the visual system blind for a short time but effectively stabilize the visual field, thereby reducing retinal image motion. Most fishes adhere to this oculomotor strategy with the exception of one species, *L. fasciatus*, where the eyes drift up to a distance of 35° following a saccade (Fritsches and Marshall, 1999). However, the drifts are slow (3–4° degrees per second), which may not degrade image quality. These drifts may be important to realign the fovea within a "preferred" frontal visual field and/or may be a byproduct of a rather loose optokinetic stabilization mechanism due to a relatively featureless upwardly directed visual field (Fritsches and Marshall, 1999; Land, 1999).

4. Specialized Sampling of the Visual Field

4.1. Areae Centrales

Almost all aquatic vertebrates examined thus far possess a specialized retinal region where subpopulations of neurons are concentrated, thereby sampling a specific part of their visual field with increased resolving power. The term *area* was originally adopted by Chievitz (1891) to describe the macula lutea of humans, a term

that was described later as an *area nasalis*, *area temporalis*, or *area centralis* in other vertebrates according to the region of the retina in which it lay. However, an *area centralis* is now defined as a concentric increase in retinal cell density in any region of the retina, most authors dispensing with the regional suffix. Sometimes associated with either a deep (convexiculate) or shallow (concaviculate) pit-like invagination in the retina termed a *fovea* (see below), an *area centralis* enables accurate fixation of the two eyes and often defines the main visual axis.

The degree of inhomogeneity across the fish retina has recently initiated detailed studies of the distribution and arrangement of subpopulations of photoreceptor and ganglion cells. Based on complementary criteria such as morphology (Reckel et al., 2001), cytochemistry (Hisatomi et al., 1997; Ishikawa et al., 1997), spectral sensitivity (Carleton et al., 2000), and, in some cases, physiology (Lasater, 1982), identification of these subpopulations has enabled more informed predictions of how each specialization may underlie behavior(s).

4.2. Photoreceptor Specializations

Based on morphology, photoreceptors have been characterized into a number of types including short and long single cones, double cones (equal and unequal), triple cones, quadruple cones, and rods. These different populations can be arranged in a variety of conformations in different species, for example, a row pattern (in the cutlips minnow, Collin et al., 1996), a twisted row pattern (in salmon, Ahlbert, 1976), a square pattern (in zebrafish, Cameron and Easter, 1995), a pentagonal pattern (in the garfish, Reckel et al., 2001), and a hexagonal pattern (in the deep-sea pearleye, Collin et al., 1998). However, all of these conformations can also be found in different regions of the same retina, for example, in the garfish *Belone belone* (Reckel et al., 2001; Fig. 8.3). Other less common arrangements include a triangular mosaic in the retina of the northern pike *Esox lucius* (Braekevelt, 1975) and four equal double cones bordering a rod in the salamanderfish *Lepidogalaxias salamandroides* (Collin and Collin, 1998). Despite this variation

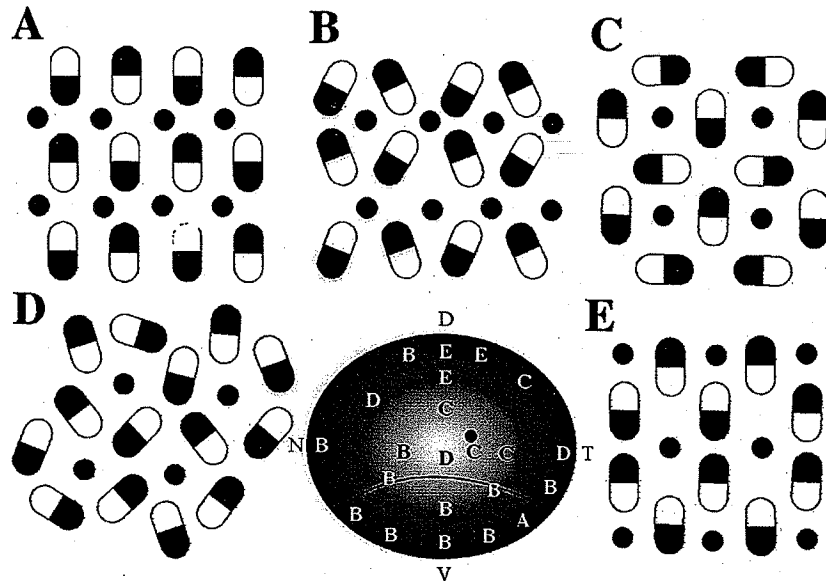


FIGURE 8.3. The diversity of retinal mosaics found throughout the retina in a single species (the garfish *Belone belone*). (A) *Pure row pattern*: Double and single cones form parallel rows. (B) *Twisted row pattern*: Double cones are twisted to form parallel rows. (C) *Square pattern*: Four double cones surround a single cone. (D) *Pentagonal pattern*: Five double cones surround a central single cone. (E)

Hexagonal pattern: Six double cones surround a central single cone. The lower middle panel shows the retina and the location of each type of mosaic. D, dorsal; N, nasal; T, temporal; V, ventral. The optic nerve head is depicted as a black circle. The line separating ventral retina is an intraocular septum (see text). (Adapted from Reckel et al., 2001.)

in sampling, little is known of the role these regular arrays play in vision. However, of all the receptor patterns described, the square mosaic comprising four double cones surrounding a central single cone appears to be relatively common and has received particular attention. Although not definitively tested, a number of theories about the function of the square mosaic have been put forward, which include increasing both visual acuity (Engström, 1963a,b; Ahlbert, 1976) and contrast (Marc and Sperling, 1976; Meer, 1994), providing a more uniform spectral sampling (Bowmaker, 1990), allowing more detailed chromatic patterns to be resolved (Lythgoe, 1979), and enhancing the detection of polarized light (Cameron and Easter, 1993; Novalés-Flamarique and Hawryshyn, 1998; Chapter 13). Although not mutually exclusive, the square mosaic may also aid in the analysis of movement in all directions in contrast to a row mosaic, which may be suited to the perception of movement in two

directions (Engström, 1963a; Anctil, 1969; Bathelt, 1970). This correlation is confirmed for a number of predatory salmonids that strike at moving prey and perceive a more three-dimensional environment using a square mosaic (Lyll, 1957a; Ahlbert, 1976; Beaudet et al., 1997) compared to schooling salmonids, which rely less on accurate strikes for prey and perceive a more two-dimensional environment along the horizontal plane using a row mosaic. The nonschooling coral trout *Plectropoma leopardus* (Collin, 1989; Fig. 8.1B), the sand-lance *Limnichthyes fasciatus* (Collin and Collin, 1988b; Fig. 8.1E), the tuskfish *Pseudolabrus miles* (Fineran and Nicol, 1974), the weeverfish *Trachinus vipera* (Kunz et al., 1985), the archerfish *Toxotes jaculatrix* (Braekevelt, 1985) and the pipefish *Corythoichthyes paxtoni* (Collin and Collin, 1999) all strike moving prey with precision in a three-dimensional environment and possess a regular square photoreceptor mosaic.

Although double cones often constitute the bulk of photoreceptors, triple and quadruple cones may also occur in large numbers in some species. Triple cones occur in two varieties, linear (e.g., in *Perca fluviatilis*) and triangular (e.g., in *Phoxinus laevis*), but their function is unknown (Lyall, 1956; Engstrom, 1960). Both quadruple and triple cones develop in central retina by the formation of subsurface cisternae along selected membrane borders of large numbers of neighboring single cones in developing black bream (Shand et al., 1999). These cone multiples fail to integrate into the regular square mosaic that predominates the retina in this species, and their central location within the retina suggests that these cone multiples are not necessarily aberrant but lie outside the influence of intercellular signaling cues that may be localized in the periphery and are responsible for the formation of the retinal mosaic during growth (Raymond, 1995; Shand et al., 1999). Interestingly, the lesioned retina of the green sunfish, *Lepomis cyanellus*, regenerates double and triple cones but is unable to reestablish the repeating cone mosaic following damage to the retina (Cameron and Easter, 1995).

Surrounded by either the retinal pigment epithelium or dense collections of tapetal material, both cones and rods may form aggregations, grouped together as macroreceptors to increase sensitivity in low light. Rods (e.g., in the weever fish *Trachinus vipera*, Kunz et al., 1985), or cones (e.g., in the pacific tarpon *Megalops cyprinoides*, McEwan, 1938), or both receptor types (e.g., in the mormyrid *Marcusenius longianalis*, Engström, 1963a, the goldeye *Hiodon alosoides*, Braäkevelt, 1982, and the featherfin *Xenomystus nigri*, Ali and Anctil, 1976) are electrically and optically isolated into groups, but the sampling advantage this pattern provides is unknown. A detailed topographic study of both the photoreceptor and ganglion cell populations in the tubular-eyed deep-sea pearleye *Scopelarchus michaelisarsii* shows that groups of rods lie in the caudal region of the main retina, where electrotonic synapses may physiologically link each receptor in the group and summate input from a large area to increase sensitivity at the expense of spatial

resolving power (Locket, 1970; Collin et al., 1998).

The large diversity in photoreceptor mosaics in different species of fishes and within different parts of the retina suggests that the environment and habitat play the most important roles in each species' sampling strategy rather than being controlled by any phylogenetic constraints. A detailed study by Reckel et al. (2001) in the garfish *Belone belone* is a case in point (Fig. 8.3). Three areas centrales are identified, a ventro-nasal (18×10^3 double cones per mm^2), a ventro-temporal (18×10^3 double cones per mm^2), and a dorso-temporal (14×10^3 double cones per mm^2) area, which mirrors the specialized zones of acute vision in the Florida garfish *Lepisosteus platyrhincus*, a species with a similar predatory lifestyle living close to the surface despite the two species being separated phylogenetically by at least 200 million years (Collin and Northcutt, 1993). The complexity of the visual environment being sampled is further emphasized by the large number of photoreceptor conformations within the one retina (e.g., in *B. belone*, Reckel et al., 2001).

The upper and lower visual fields of most species are very different but none more so than those species that exist near the surface of the water, such as the garfish *Belone belone*. In this unique environment, coping with high light intensities, avoiding predation and the refractive problems associated with seeing through the surface of the water (into Snell's window) must be overcome by the ventral retina, while the need to optimize sensitivity in often low light intensities must be accomplished by the dorsal retina. In *B. belone*, the upper and lower visual fields are sampled by a twisted row and a hexagonal array pattern of cone photoreceptors, respectively (Reckel et al., 2001; Fig. 8.3). As in the osteoglossid *Pantodon buchholzi* (Saidel, 1987), *B. belone* also possesses an intraocular septum that divides the dorsal and ventral retinal regions and inhibits the refractive disturbances associated with the borders of Snell's window (Schwartz, 1971; Fig. 8.3). In the pelagic blue marlin *Makaira nigricans*, the ventral retina contains a square mosaic, while the dorsal retina that peers into dim, monochromatic light possesses a row mosaic

(Fritsches et al., 2000). Marked differences in retinomotor movements (Reckel et al., 2001), tapetal material (Collin, 1988; Collin and Northcutt, 1993; Takei and Somiya, 2001), and optomotor control (Saidel and Fabiane, 1998; Saidel, 2000) between the dorsal and ventral retina reflect a divergence in spatial (finding a compromise between resolving power and sensitivity) and chromatic sampling.

Cone types characterized by the spectral sensitivity of their visual pigments govern chromatic sampling. The wavelength of maximum absorbance of a visual pigment (λ_{\max}) is dependent on the amino acid sequence of the opsin protein and the interaction with its associated chromophore, which may be based on either rhodopsin (the aldehyde of vitamin A₁) or porphyropsin (the aldehyde of vitamin A₂). Concomitant with morphological variations, the opsin expressed within each photoreceptor type also varies and can be classified into one of five evolutionarily distinct groups of vertebrate visual pigments (Yokoyama, 1997). Changes in spectral sensitivity across species or within species during development (as discussed further below) are mediated by different ratios of the two chromophores (see review by Loew, 1995) and/or variations in the expression of genes coding the opsin protein (Carleton and Kocher, 2001; J. Shand and N. Thomas unpublished). Just as the density of specific cone types (based on morphology) varies across the retina and dictates changes in spatial resolving power, the spectral sensitivity of chromatic sampling units also varies, and can be related to the spectral transmission of light through the water from different regions of the visual field (Levine and MacNicol, 1979).

4.3. Ganglion Cell Specializations

In general, the topography of the ganglion cell population is closely aligned with the topography of the photoreceptor population, although few studies have compared both within the same species. Ganglion cell densities in reef teleosts range from a peak of 6×10^3 cells per mm² in the frogfish *Halophryne diemensis*, a lie-in-wait predator (Collin and Pettigrew,

1988a), to over 150×10^3 cells per mm² in the sandlance *Limnichthyes fasciatus*, a predator that launches its whole body to engulf its prey (Collin and Collin, 1988c; Pettigrew and Collin, 1995). The spacing of the ganglion cells dictates the spatial resolving power of the eye and has a close relationship to the behavioral acuity (Fig. 8.4). The spatial resolving power in reef fishes has been found to vary from 4 to 27 cycles per degree, respectively (Collin and Pettigrew, 1989). Although *H. diemensis* and *L. fasciatus* possess an area centralis in the middle of the retina, where the eyes subtend a large binocular overlap, in species with lateral eyes, the temporal retina is the most commonly specialized region for acute vision, subtending a part of the frontal visual field (Fig. 8.5). However, some fishes possess more than one acute zone, mediating increased spatial resolving power in different parts of the visual field (Collin and Pettigrew, 1989; Fig. 8.5). Some balistids possess both a temporal and a nasal area centralis for feeding and swimming backward, respectively (Ito and Murakami, 1984; Collin and Pettigrew, 1988b). Once thought to be devoid of any retinal specialization (Johns and Easter, 1977), the goldfish *Carassius auratus* has been found to possess a temporal area centralis with respect to both ganglion cell (Mednick and Springer, 1988) and photoreceptor (Mednick et al., 1988) densities, but many other species of cyprinids possess up to three areas (Zaunreiter et al., 1991; Collin and Ali, 1994).

In addition to photoreceptor arrays, other cell types including ganglion cells also form regular mosaics that effectively sample all parts of the eyes' visual field and may have specific functions. Recent studies have identified a subset of large ganglion cells with large soma (Fig. 8.4B), extensive dendritic fields, and terminal stratification within different levels of the inner plexiform layer (IPL). These have been identified in a range of fishes (Cook et al., 1999) and, although not unequivocally established, may have functional and evolutionary homologies to the large cells described for amphibians (Shamim et al., 1997) and mammals (Boycott and Wässle, 1974). On morphological criteria, these cells appear comparable to the alpha or Y class cells described in cats by Wässle et al.

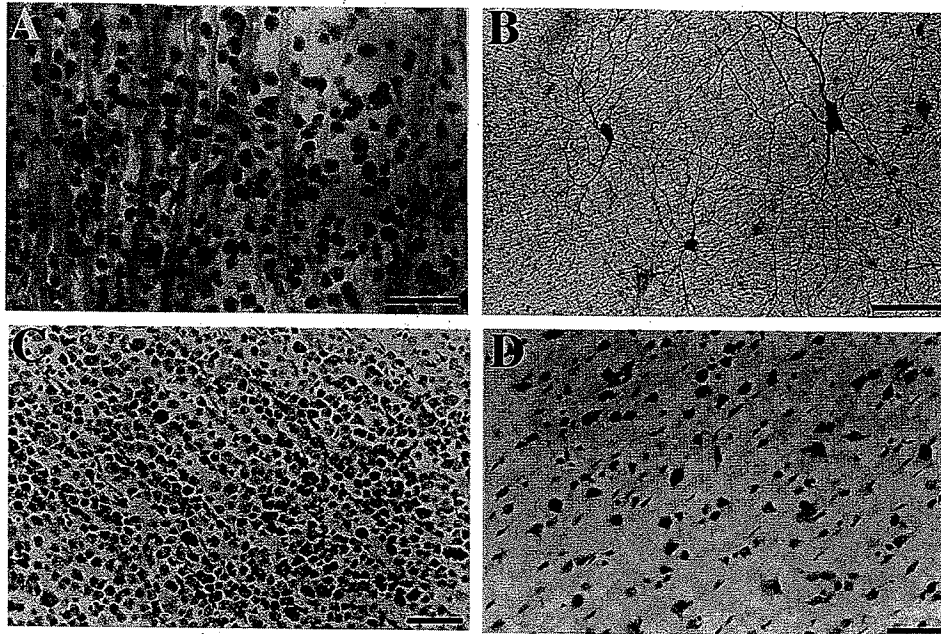


FIGURE 8.4. Ganglion cell sampling of the visual field. (A) Ganglion cells of the Florida garfish *Lepisosteus platyrhincus* retrogradely labeled with horseradish peroxidase from the optic nerve. Bundles of axons separate the cells into columns. (B) Giant ganglion cells retrogradely labeled with cobaltous lysine in the garfish showing the large den-

dritic fields of these alpha-like cells that form regular mosaics across the retina. (C, D) Ganglion cells of the black bream *Acanthopagrus butcheri* in the area centralis (C) and peripheral (D) regions of the retina. (Adapted from Shand et al., 2000a). Scale bars, 20 μm (A); 100 μm (B); 50 μm (C); 50 μm (D).

(1981) and therefore may be motion sensitive with brisk transient receptive fields. These large ganglion cells can be divided into subgroups: cells that stratify within the vitread (inner or ON cells), sclerad (outer or OFF cells) (Cook and Becker, 1991; Cook et al., 1992; Collin and Northcutt, 1993), middle (Cook and Sharma, 1995), and within both the inner and middle laminae of the IPL (Cook et al., 1999). Although these cells represent less than 1% of the ganglion cell population, each subtype forms a spatially independent mosaic providing full coverage of the retina and therefore the visual field (albeit at low density), despite having soma "displaced" into the inner nuclear layer. Regular arrays of bplexiform ganglion cells have also been discovered in both lampreys (Fritzsche and Collin, 1990) and bony fishes (Hitchcock and Easter, 1986; Cook et al., 1996), suggesting that, like the alpha cells, cel-

ular mosaics may be a common feature of most vertebrate classes. The relationship between the mechanisms underlying the elaboration of dendritic arbors and the patterning of cell bodies still remains theoretical (Cook and Chalupa, 2000), however, the finding of regular arrays of cells confined to specific retinal regions (e.g., temporal retina, see below) suggests that, in some species, these cells may have specific functions relevant to their lifestyle.

4.4. The Area Giganto Cellularis

In contrast to the contiguous dendritic fields of large (alpha-like) ganglion cells that cover the entire retina, and therefore subtend all of the visual field in the shallow-water fishes described above, there are a group of deep-sea fishes that possess a regular array of large ganglion cells restricted to temporal retina. In the

pearleye *Scopelarchus michaelisarsi* (Collin et al., 1998) and the daggertooth *Anotopterus pharao* (Uemura et al., 2000), the aptly named area gigantea centralis (AGC) is comprised of large soma with dendritic terminals stratifying within the outer and inner parts of the IPL, respectively. Due to their size and large dendritic field, these cells are thought to be motion sensitive to objects crossing the binocular visual field. The difference in dendritic stratification between the two species may be related to the background illumination, where the ON-type cells of *S. michaelisarsi* may respond to a bright point source of bioluminescent light against a dark background and the OFF-type cells of *A.*

pharao may respond to a silhouetted prey item against the bright background of downwelling skylight (the daggertooth adopts a head-up posture within the water column, Collin et al., 1998; Uemura et al., 2000). Interestingly, an AGC comprising ON-type cells has also been described in the temporal retina of five species of procellariform sea birds, which feed on prey moving against a dark background (Hayes et al., 1991).

4.5. Horizontal Streaks

Chievitz (1889, 1891) and Slonaker (1897) were the first to describe horizontal band-shaped

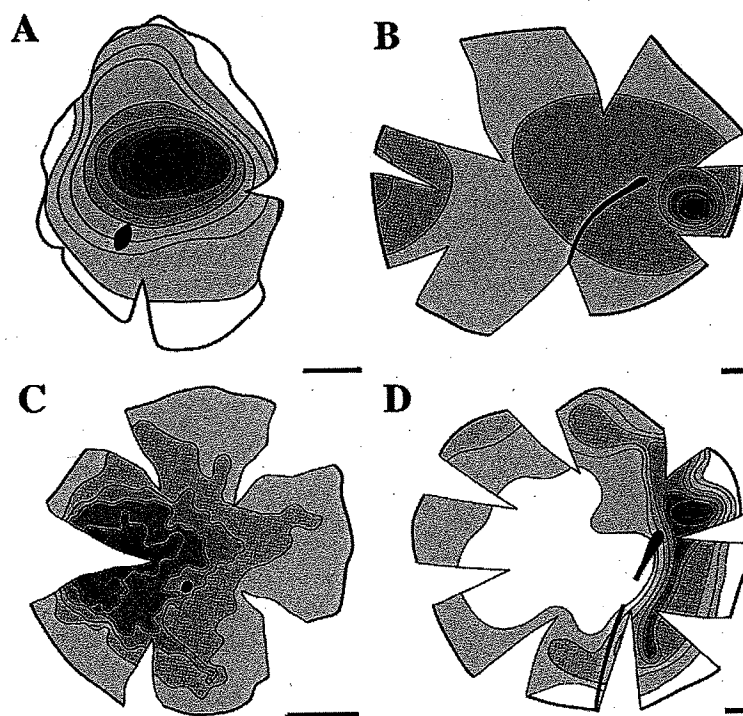


FIGURE 8.5. Ganglion cell specializations (areae centrales). (A) The sandlance *Limnichthyes fasciatus* (<50.0 to 150.0×10^3 ganglion cells per mm^2). (B) The coral cod *Cephalopholis miniatus* (<10.0 to 47.0×10^3 ganglion cells per mm^2). (C) The cookie-cutter shark *Isistius brasiliensis* (<0.8 to 1.6×10^3 ganglion cells per mm^2). (D) The deep-water bass *Howella sherborni* (<12.0 to 24.0×10^3 ganglion cells per mm^2). Note the concentric arrangement of iso-density contours with the exception of *H. sherborni*, which has

a vertical streak. The optic nerve head and falciform process (where present) is depicted in black. The progressively darker shading represents increases in cell density. Dorsal is toward the top and the area centralis is located in temporal retina in each species with the exception of *L. fasciatus*. Scale bars, 1.0 mm (A, B); 5 mm (C); 1 mm (D). (Adapted from Collin and Collin, 1988a (A); Collin and Pettigrew, 1988a (B); Bozzano and Collin, 2000 (C); Collin, 1997 (D)).

retinal area in bony fishes and these specializations or visual streaks can take two forms: either a band-shaped increase in thickness across the retinal meridian, as found in the cyprinodontid *Fundulus heteroclitus* (Butcher, 1938) and two species of mudskippers, *Boleophthalmus* and *Periophthalmus* (Munk, 1970), or simply a marked increase in ganglion and photoreceptor cell density as found in the balistids, *Navodon modestus* (Ito and Murakami, 1984) and *Balistoides conspicillum* (Collin and Pettigrew, 1988b) and the yellow-finned trevally, *Caranx ignobilis* (Collin, 1999; Fig. 8.6). The visual streak can be pronounced

(e.g., a peak of over 90.0×10^3 ganglion cells per mm^2 in *C. ignobilis* and a centroperipheral gradient of 10:1, Collin, 1997) or weak (peak of 0.93×10^3 cells per mm^2 with a centroperipheral gradient of 1.8:1 in the velvet belly dogfish *Etmopterus spinax* (Bozzano and Collin, 2000; Fig. 8.6).

The area of the visual field subtended by a streak shows interspecific variation. Most are horizontal, maintaining a retinal seam of high spatial resolving power across the central meridian that allows a panoramic sampling of an elongated region of the lateral visual field. However, upwardly and downwardly directed

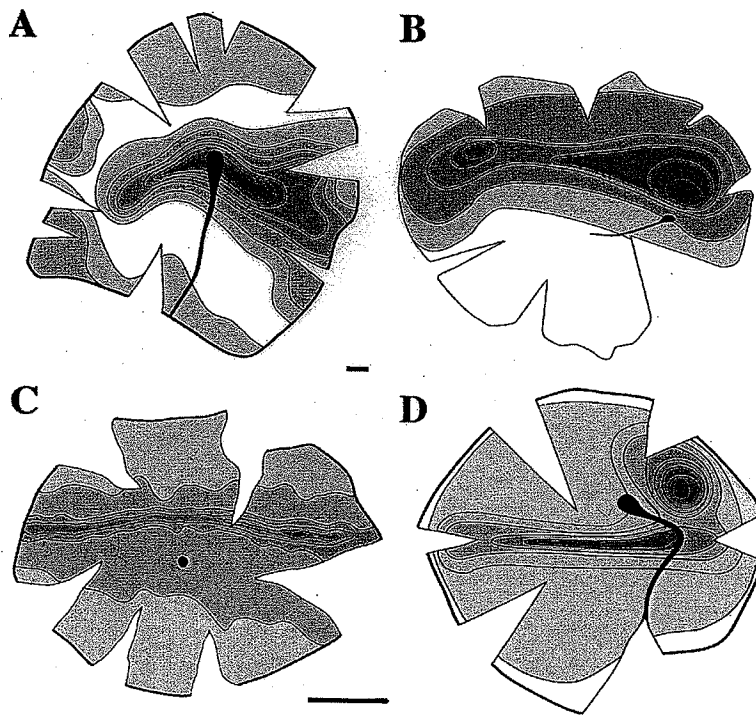


FIGURE 8.6. Ganglion cell specializations (horizontal streaks). (A) The trevally *Caranx ignobilis* (<10.0 to 90.0×10^3 ganglion cells per mm^2). (B) The weaverfish *Parapercis cylindrica* (<5.0 to 40.0×10^3 ganglion cells per mm^2). (C) The small-spotted dogfish *Scyliorhinus canicula* (<0.5 to 2.4×10^3 ganglion cells per mm^2). (D) The blue tuskfish *Choerodon albigena* (<10.0 to 83.0×10^3 ganglion cells per mm^2). Note the elongated iso-density contours across the retina, which may subtend both dorsal and ventral hemifields. Note that the streak is often associated with a

second specialization located either within the visual streak or often in temporal retina. The optic nerve head and falciform process (where present) is depicted in black. The progressively darker shading represents increases in cell density. Dorsal is toward the top and the area centralis (where present) is located in temporal retina in each species. Scale bars, 0.25 mm (A); 1 mm (B); 5 mm (C); 1 mm (D). (Adapted from Collin, 1997 (A); Collin and Pettigrew, 1988a (B); Bozzano and Collin, 2000 (C); Collin and Pettigrew, 1988b (D)).

streaks are also found in ventral and dorsal retina, respectively (Fig. 8.6). The Florida garfish, *Lepisosteus platyrhincus*, possesses a visual streak (9.40×10^3 ganglion cells per mm^2) across the ventral meridian of the eye in conjunction with a temporal area centralis (6.25×10^3 cells per mm^2). The horizontal streak subtends the surface of the water, which it uses as a background to prey upon live fishes with its long snout, armed with needle-like teeth (Collin and Northcutt, 1993). A population of "displaced" ganglion cells situated in the inner nuclear layer is also concentrated into a ventral visual streak (6.25×10^3 cells per mm^2) in the garfish retina. This ectopic streak is inflected 20° from the horizontal and may provide a finer control for the stabilization of the retina during compensatory eye movements, while the temporal area centralis could provide an increase in visual acuity for prey observed in frontal visual space. Interspecific differences in the location of the streak also occur in cartilaginous fishes, where the position of the eyes within the head and the visual axis vary markedly among the three major groups: batoids, selachians, and the chimaerids (Bozzano and Collin, 2000; Fig. 8.6).

Many species of ray-finned fishes possess a retinal specialization in addition to a visual streak. In the blue tuskfish *Choerodon albigena* and the red-throated emperor *Lethrinus chrysostomus*, a temporal area centralis lies in conjunction with a horizontal streak (Collin and Pettigrew, 1988b; Fig. 8.6). The existence of two specializations subtending different regions of the visual field suggests that each may provide a specific sampling strategy, especially when each specialization is comprised of cells of different morphology and receptive field size (Collin, 1989). In *Aplocheilichthys lineatus* and *Epiplatys grahami*, which prey upon insects that lie trapped in the surface film of the water (Munk, 1970), each retina contains two band-shaped thickenings across the horizontal meridian. These central band-shaped areas, although both oriented parallel to the surface of the water, are separated by 40° and subtend different regions of the visual field. It is assumed that the upper band is able to view lateral visual field in search of food within the water column,

while the lower (ventral) band is able to detect prey venturing into the edges of Snell's window (Munk, 1970).

The visual streak may have various functions. Thus far, the horizon (either the sand-water or air-water interface) has predominated the visual field of each species of ray-finned fishes found to possess a horizontal streak (Collin and Pettigrew, 1988a,b). A panoramic view of the visual field sampled with increased spatial resolving power negates the need for the saccadic eye movements necessary using an area centralis. Disturbances in the horizontal part of the visual field subtended by a streak will also lower the threshold for the perception of movement and signal either prey or predator. Where the symmetry of the visual world is particularly two-dimensional, but there is some need for higher spatial resolving power within a specific part of the visual field, a compromise is reached where a cell density peak lies within a visual streak (Yew et al., 1984; Bozzano and Collin, 2000; Fig. 8.6).

4.6. Foveae

Shallow foveae in the eyes of bony fishes were noted over 100 years ago (Slonaker, 1897). Later, Kahmann (1934) identified a large number of species with deep foveae located predominantly in temporal retina and mediating acute binocular vision. Foveae were always associated with fixating eye movements and, in a few species, foveal location varied with the position of the eyes in the head, sometimes mediating monocular vision.

More recently, the relationship between the presence of a fovea and increased eye mobility has been noted in a number of teleosts, including the kelp bass *Paralabrax clathratus* (Schwassmann, 1968), the sandlance *Limnichthys fasciatus* (Pettigrew and Collin, 1995), the clingfish *Gobiesox strumosus* (Wagner et al., 1976), and the sandperch *Parapercis nebulosus* (Easter, 1992). Over 42 species of bony fishes that frequent shallow water have been found to possess foveae (reviewed in Collin and Collin, 1999). The teleost fovea is an indentation of the retina (Fig. 8.7) and, thus far, has always been associated with an increase in

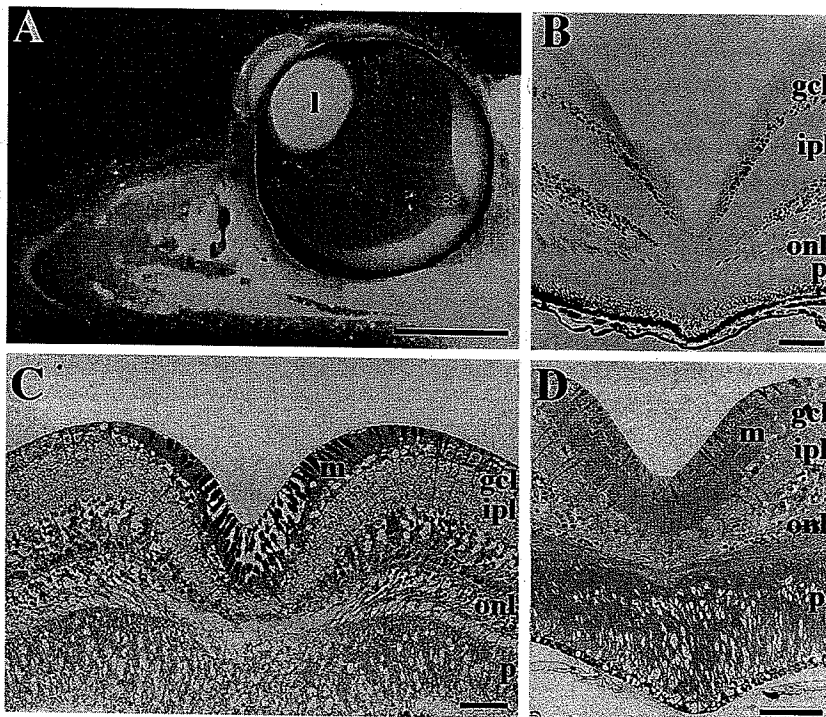


FIGURE 8.7. Fovea in bony fish. (A) A frozen section of the head of the sandlance *Limnichthyes fasciatus* in the sagittal plane showing the depth of the convexiclivate fovea (*) in the eye, the nonspherical lens (l), and the corneal lenticle, all aligned along the visual axis. (B) A resin section of the sandlance fovea showing the displacement of the inner retinal layers. (C, D) Transverse sections of the fovea in the deep-sea smoothheads *Conocara murrayi* (C) and, C.

macroptera (D). Note the thick foveal lining of Müller cell processes (m) and the elongation of the photoreceptors beneath the foveal clivus. gcl, ganglion cell layer; ipl, inner plexiform layer; onl, outer nuclear layer; p, photoreceptor layer. Scale bars, 0.5 mm (A); 50 μ m (B); 100 μ m (C, D). (B is adapted from Collin and Collin, 1988c, and D is adapted from Collin et al., 2000.)

both photoreceptor and ganglion cell density (area centralis), although a clivus in the otherwise smooth retinal surface lining the eyecup predicts that the fovea also provides an optical advantage.

One optical advantage of a convexiclivate fovea (Munk, 1975; Collin and Collin, 1988b,c) may be image magnification resulting from a marked change in refractive index between the vitreous and the sloping sides of the fovea, thereby increasing visual resolution (Walls, 1937, 1940, 1942; Snyder and Miller, 1978; Locket, 1992; Collin et al., 1994). The fovea may play a major role in the detection and maintenance of fixation, providing an increased sensi-

tivity to small angular movement as the image of a moving object is distorted by the curvature of the pit (Pumphrey, 1948). In conjunction with a high degree of independent eye mobility, a deep foveal pit may also act as a directional and monocular indicator of accommodative focus as has been found in the chameleon (Harkness and Bennett-Clarke, 1978) and in the marine sandlance (Pettigrew and Collin, 1995). Where the foveal axes fall within a pronounced binocular overlap, skewing of eccentric images may also provide a useful cue about range and possibly a method of breaking luminescent camouflage in a number of foveate teleosts, which have ventured into the deep-sea (Steenstrup

and Munk, 1980; Locket, 1985, 1992; Wagner et al., 1998).

Based on morphological, ecological, and functional diversity, the teleost fovea has recently been characterized into at least four distinct types (Collin and Collin, 1999). Type I is exemplified by the syngnathid fovea, such as that in *Corythoichthyes paxtoni*, and is characterized by a steep-sided (convexiclvate) retinal pit without a lateral displacement of the inner retinal layers (Collin and Collin, 1999). A Type II fovea is also convexiclvate but the inner retinal layers are displaced laterally, leaving an unimpeded path for the incident light to strike the underlying photoreceptors. Examples of a Type II fovea are found in the sand-lance, *Limnichthyes fasciatus* (Collin and Collin, 1988b,c; Fig. 8.7A,B) and the notosudid, *Scopelosaurus hoedti* (Munk, 1975). Type III foveae are similarly convexiclvate but possess a thick foveal lining of radial fiber processes putatively thought to be refractive. Examples of this foveal type are found in the deep-sea alepocephalids, *Conocara macroptera* (Collin et al., 1994; Wagner et al., 1998; Fig. 8.7C,D) and *Alepocephalus bairdii* (Locket, 1992). Although changes in refractive index within foveal and perifoveal retinal regions still need to be examined, indices of 1.3353 (vitreous) and 1.3494 (retina) measured in *Chondrostoma nasus* (Nicol, 1989) suggest that this gradation may produce refraction. Changes in foveal thickness, the displacement of the inner retinal layers, and variations in the shape of the foveal clivus may also produce different optical effects to satisfy specific ecological needs. Type III foveae may prove to be of particular interest given the widespread occurrence of the foveal lining in other vertebrates, such as birds (Locket, 1992), where the relative thickness of the dense radial fiber processes may comprise up to 40% of the foveal thickness (Locket, 1992; Wagner et al., 1998). Finally, the Type IV fovea is a shallow (concaviclivate) invagination of the retina where there is neither a lateral displacement of inner retinal layers nor a radial fiber lining. Examples of this type are found in the banded toado, *Sphaeroides pleurostictus* (Collin, 1987), and the deep-sea *Bathylagus benedicti* (Vilter, 1954).

5. Sampling a Changing Visual Environment

Many aquatic animals undergo dramatic changes in their visual environment during development, changes frequently associated with an alteration in feeding behavior. The transition of amphibians from an aquatic to a terrestrial habitat at metamorphosis imposes different optical demands, as does the migration of fishes between different bodies of water, resulting in the need to change their visual axis or spectral sampling. The reason that migration between different aquatic habitats results in pronounced changes in visual environment relates to the variable physical constraints that are imposed on the transmission of light in different bodies of water and at different depths. For example, as surface-living larval fishes metamorphose and move deeper in the water column, there will be a concomitant reduction in both the intensity and spectral composition of the ambient light. Similarly, anadromous migrations between the sea and freshwater for the purposes of maturation and breeding result in animals inhabiting an environment with very different spectral qualities. Where changes in feeding behavior take place, there may also be a need to change the main visual axis and retinal sampling array.

5.1. The Relationship Between Changing Visual Demands and the Visual Field

In general terms, prey species require a wide field of view to scan the visual scene, whereas predators often require a large overlap in the visual fields of both eyes to increase binocularity (Lythgoe, 1979). As tadpoles, frogs possess a wide monocular field of view in water but increase their binocular overlap to allow for depth perception and the detection of insectivorous prey on land (Sivak and Warburg, 1983). Migrations from aquatic to aerial habitats are also accompanied by optical changes to counteract the increased refractive power of the cornea in air (Sivak, 1988; Collin and Collin, 2001).

Despite avoiding the optical problems associated with a transition from an aquatic to an aerial lifestyle, developmental changes in feeding behavior of fishes can result in changes in the visual axis. The migration of the eyes in the head in flatfishes is perhaps the most dramatic. In the early stages of development, pelagic larvae feeding on plankton in the water column possess laterally placed eyes. During the transition to a benthic existence, instead of a dorso-ventral flattening of the body as seen in cartilaginous skates, flatfishes move the left (e.g., sole) or right (e.g., flounder) eye to the other side of the head. As adults, the fishes lie on their sides on the substrate with both eyes directed upward, subtending a large binocular overlap (Beaudet and Hawryshyn, 1999).

Metamorphosis in other pelagic larval fishes may be less radical, but it is likely there will be changes in the visual field associated with changes in feeding behavior following settlement. For example, during the transition from a pelagic juvenile stage, where they feed on plankton in the water column, goatfishes settle onto inter-reef substrate, where they begin using sensory chin barbels to disturb invertebrates from the sediment (McCormick, 1993). During this metamorphosis, the goatfish undergoes changes in head and body shape and the eyes move dorsally (J. Shand, unpublished). Similarly black bream, *Acanthopagrus butcheri*, alter the axis of maximal binocular overlap from 30° to 50° below the horizontal axis as they move out of the water column to become benthic feeders (S.P. Collin, K. Doving, and J. Shand, unpublished; Fig. 8.2E,F). The part of the visual field subtended by the two eyes changes from dorsal to ventral in the Australian lungfish, *Neoceratodus forsteri* (S.P. Collin and J. Joss, unpublished). In larval clown fish, *Premnas biaculeatus*, the functional visual field rapidly increases in the horizontal plane as shown by feeding experiments that record the position of the prey relative to the eye when the prey is first detected (Job and Bellwood, 1996). Eels are also known to increase the size of their eyes, and the size of their visual field, prior to migration into deeper waters for breeding (Pankhurst, 1982).

5.2. Changes in Photoreceptor Complement and the Cone Mosaic During Ontogeny

The retinal cone photoreceptors of fishes can be arranged in a number of different repeating arrays, which have been related to different sampling tasks (see Section 4.2). However, if visual demands change, it may be advantageous to alter the arrangement of the cone mosaic. Until recently, any changes to the mosaic have been attributed to either a loss or addition of cones rather than any reorganization. For example, during smoltification in salmonids, the single cones at the corner of the mosaic are lost (Lyall, 1957b; Ahlbert, 1976; Bowmaker and Kunz, 1987; Hawryshyn et al., 1989) or cease to be incorporated into the retina (Novales-Flamarique, 2001) between the parr and adult stages. However, in a recent study of the rainbow trout, changes in the cross-sectional shape of double cones have been found to alter the mosaic formation from a square to a row arrangement (Novales-Flamarique, 2001).

Many marine fishes hatch with only single cones arranged in a hexagonal (or row) mosaic, presumably to optimize packing and maximize acuity in small eyes (Blaxter, 1986; Evans and Fernald, 1993; Pankhurst et al., 1993; Shand et al., 1999). New cones are added during growth and double cones are formed at a later stage by the association of large numbers of neighboring single cones and the formation of subsurface cisternae along the common membranes (Shand et al., 1999, 2001). At the time of double cone formation, the hexagonal mosaic of single cones breaks down and, at least in black bream, a square mosaic comprising four double cones surrounding a single cone eventually results (Fig. 8.8).

Acuity in larval fishes rapidly increases as the eye and lens grow, producing an increase in the magnification of the image on the retina (Fernald, 1988; Shand, 1997). Sensitivity is improved as the photoreceptors increase in size, as new cones are differentiated and added at the retinal periphery and as rods are inserted throughout the retina (van der Meer, 1994; Poling and Fuiman, 1997; Fuiman and Delbos,

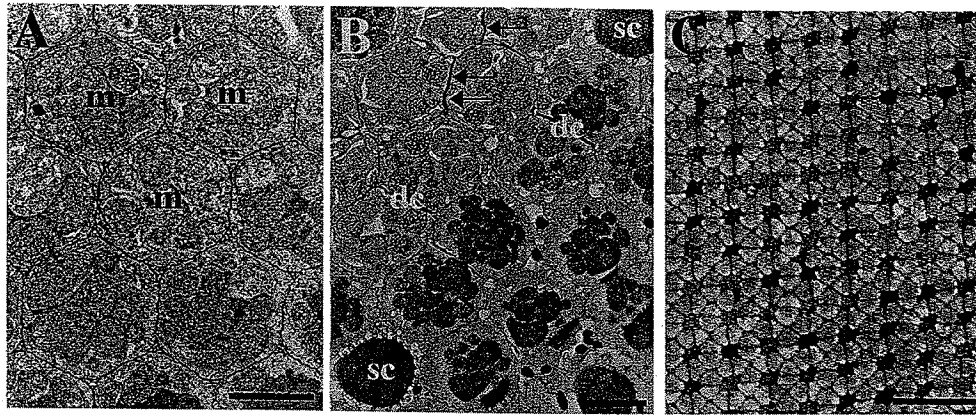


FIGURE 8.8. Development of a square cone mosaic. (A) Electron micrograph of the retina in a 3–5 mm standard length (SL) black bream *Acanthopagrus butcheri* showing the regular hexagonal array of a single morphological class of photoreceptor in tangential section. (B) Tangential section of the retina of a black bream of 8 mm SL showing cone multiples

with subsurface cisternae along their apposing membranes (arrows) interrupted by single cones (sc). (C) The regular array of the square mosaic in a black bream of 30 mm SL where four double cones surround a central single cone (dark profiles). dc, double cone; m, mitochondria. Scale bars, 2 μ m (A, B); 20 μ m (C). (Adapted from Shand et al., 1999).

1998; Pankhurst and Hilder, 1998). The developmental changes in the complement and number of photoreceptors resulting in greater sensitivity provides the potential for migration to progressively lower light intensity habitats. For example, larval cardinal fishes (Apogonidae) are able to feed at greater depths than other coral reef fish larvae of a similar age due to the presence of larger double cones and a greater rate of addition of new rods (Shand, 1997; Job and Bellwood, 2000; Job and Shand, 2001). Similarly, dhufish *Glaucosoma hebraicum* rapidly increase both the length of their cones and their rod densities from an early stage of retinal development as they move into deeper water (Shand et al., 2001). Ontogenetic migration to a habitat with lower light intensity can also result in the reduction or loss of cones and an increase in rod density to enhance sensitivity. For example, in the surface-living juveniles of *Sebastes diploproa* (Boehlert, 1979) and *Gempylus serpens* (Munk, 1990) the cones are lost as the fishes mature and move into deep water. Another possible mechanism for increasing sensitivity during development is observed in the southern hemisphere lamprey *Geotria australis*, as

it returns to the heavily tannin-stained rivers for spawning. The ellipsoid region of one of the cone photoreceptors develops a large transparent ellipsosome, which may gather and focus light onto the outer segment (Collin et al., 1999).

5.3. Spectral Sampling and Visual Pigment Changes

Particular combinations of visual pigments appear to be “suited” for the detection of contrast in different bodies of water (Lythgoe and Partridge, 1989, 1991; Chapter 17). Therefore, it is perhaps not surprising that during migration or development, concomitant changes in spectral sensitivity that match the changes in the photic environment have also been found in a number of species. The changes in spectral sensitivity can result from structural modifications in the retina or physiological changes to the visual pigments themselves.

The loss of single cones from the corners of the cone mosaic, mentioned above, has been correlated with the loss of ultraviolet (UV) sensitivity as fishes move into deeper water, switch from a planktivorous to a benthopelagic exist-

tence, or begin their migration to the ocean (Bowmaker and Kunz, 1987; Hawryshyn et al., 1989; Loew and Wahl, 1991). In the salmonid, *Oncorhynchus mykiss*, the loss of single cones appears to affect only the ventral retina. UV sensitivity is known to reappear when the fishes return to the rivers, however, it is not known if new cones are regenerated in ventral retina or whether the sensitivity results from the population of single cones that remains in dorsal retina (Hawryshyn et al., 1989; Brownman and Hawryshyn, 1992; Beaudet et al., 1993; Deutschlander et al., 2001).

Changes in the physiology of the visual pigments can bring about changes in their absorption characteristics by two main mechanisms: either a change from one chromophore to another or a switch in opsin expression (Loew, 1995 for review). Opsins with the A_2 chromophore absorb at longer wavelengths than their A_1 analogue, and the difference is greatest at long wavelengths (Dartnall and Lythgoe, 1965; Whitmore and Bowmaker, 1989; Parry and Bowmaker, 2000). Hence species inhabiting long wavelength-transmitting estuarine or freshwater frequently possess A_2 (porphyropsin)-based visual pigments. Conversely, the majority of marine species possess A_1 (rhodopsin)-based visual pigments (Wald, 1939; Lythgoe, 1979; Bowmaker, 1995). Wald (1958), after examining lampreys and eels, came to the conclusion that species undergoing metamorphosis and moving between marine and freshwater switched from A_1 to A_2 and vice versa. Examples of species switching either their chromophores, or the proportion of A_1 to A_2 , during migration include salmonids (Beatty, 1966), eels (Carlisle and Denton, 1959; Beatty, 1975), and lampreys (Crescitelli, 1956). Many species of cyprinids, whose habitats can be spectrally variable on a seasonal basis, possess a mixture of both chromophores, and the ratio of the two pigments can vary according to environmental conditions such as day length and temperature (see Beatty, 1984; Muntz and Mouat, 1984; Whitmore and Bowmaker, 1989).

Changes in rod opsin structure are also possible in combination with chromophore changes, as demonstrated in eels as they migrate either into deep marine water (Carlisle and

Denton, 1959; Beatty, 1975) or into freshwater (Wood et al., 1992) habitats, where the peak absorption (λ_{\max}) shifts to shorter and longer wavelengths, respectively. Opsin substitutions have also been monitored within individual rods in eels (Wood and Partridge, 1993) and inferred in the rods of the deep-sea pearleye, *Scoperlarchus analis* (Partridge et al., 1992).

In developing marine fishes, changes in cone opsin structure have been inferred in retinæ containing purely A_1 -based visual pigments. During the larval/juvenile transition in the winter flounder, *Pseudopleuronectes americanus*, only single cones with a λ_{\max} at 520 nm are present, whereas in adults three different visual pigments occur with λ_{\max} values at 457, 531, and 547 nm (Evans et al., 1993). In the pollack, *Pollachius pollachius*, the λ_{\max} of the single cones shifts from violet (420 nm) to blue (460 nm) as the fishes migrate to deeper green-transmitting coastal water during growth (Shand et al., 1988). Similarly, in the goatfish, *Upeneus tragula*, double cones lose red sensitivity by shifting the λ_{\max} of the double cones from a 487/580 nm pair to a 515/530 nm pair as the fishes leave the broad spectrum surface waters to take up a benthic habitat with reduced proportions of red light (Shand, 1993). In the estuarine black bream *Acanthopagrus butcheri*, the λ_{\max} of both single and double cones changes as they migrate to deeper, predominantly red-transmitting, tannin-stained water and begin feeding from the substrate (Shand et al., 2002). In the bream, the short wavelength-sensitive single cones shift their λ_{\max} from 420 to 480 nm and the medium wavelength-sensitive double cones from about 530 to 565 nm (Fig. 8.9). While all the above changes in visual pigments can be rationalized in terms of improving the efficiency of vision in differing spectral environments, the exact mechanisms that initiate and bring about the changes from one opsin to another are presently unknown.

Until recently, the spectral sensitivity of cones in early stage larval fishes has been unclear. The possession of only one morphological cone type (single cones) suggests the presence of only one visual pigment (Evans et al., 1993; Loew and Sillman, 1993). However, it

ater
eak
iger
ons
lual
and
eye,

one
ae
nts.
the
ri-
am
ent
57,
he
of
er
th
h,
si-
es
as
ce
th
)
is
le
r,
d
e
t
r
n
t
e
l
l
t
;

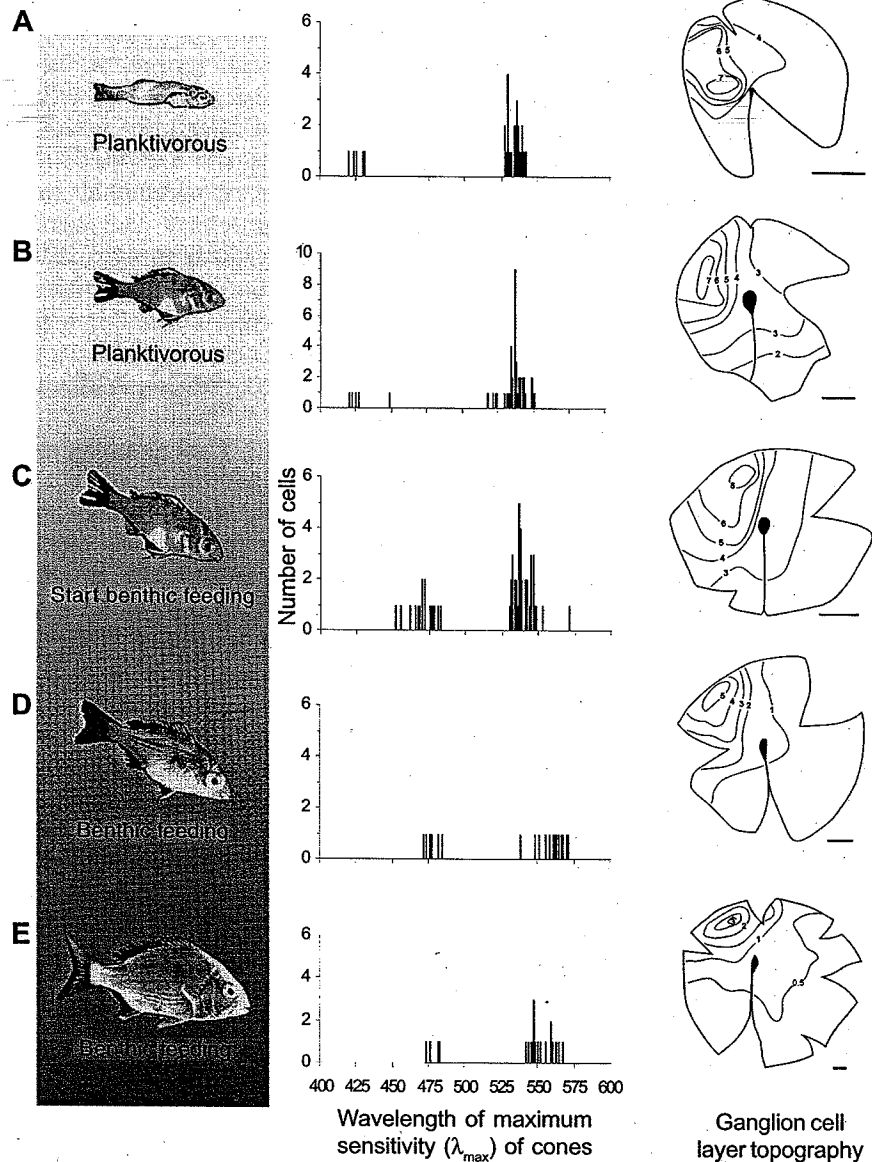


FIGURE 8.9. Summary of behavioral and visual changes in the black bream *Acanthopagrus butcheri*, during juvenile transition. The larvae and juveniles younger than 100 days (A, B) are primarily shallow-water plankton feeders, but gradually begin feeding from the substrate in deeper tannin-stained estuarine water (C). Concomitant with the behavioral changes, the visual pigments of the cones have been found to

shift to longer wavelengths (frequency histograms of λ_{max} records from individual cones) as the position of the ganglion cell area centralis relocates from the temporal to the dorso-temporal region of the retina by 170 days of age (D) (retinal topography maps of right eyes) and become similar to adults (E). Scale bars, 1 mm. Cell densities $\times 10^4$ per mm^2 . See text for further details.

is now apparent that at least two visual pigments are present in the retinae of many marine larval fishes when there is only one cone type present (Britt et al., 2001; Helvick et al.,

2001; Shand et al., 2002). The majority of cones are medium wavelength (green) sensitive and would increase sensitivity to the predominant wavelengths transmitted in coastal waters. The

second visual pigment appears to be short wavelength (either violet or UV) sensitive. The possession of a short wavelength-sensitive pigment may be an aid to planktivory in a shallow-water environment rich in UV wavelengths where zooplankton either reflect or absorb UV light (Bowmaker, 1991; Novales-Flamarique and Browman, 2001). Indeed, UV light has been found to facilitate plankton feeding (Loew et al., 1993; Browman et al., 1994) and several adult planktivorous fishes have also been found to possess UV-sensitive visual pigments (McFarland and Loew, 1994). From *in situ* opsin labeling in larval halibut, UV sensitivity is observed in only the ventral retina, which may be useful in feeding on plankton in the upper visual field (Helvick et al., 2001).

In the black bream, no changes in visual pigments are observed at the time the double cones are formed and the cone mosaic is reorganized (Shand et al., 2002; Figs. 8.8, 8.9). Changes in visual pigments occur only when behavioral and habitat transitions are underway (Shand et al., 2002; Fig. 8.9). However, individual variability in the timing of visual pigment changes was observed, where fishes reared in tannin-stained water or caught from tannin-stained estuaries undergo these changes at an earlier stage than those reared in clear water (J. Shand and N. Thomas unpublished). The individual variability may reflect the ability for species living in unstable environments, such as estuaries, to respond to changing conditions. However, previous light history has now also been shown to affect feeding ability of the larvae of striped trumpeter, *Latris lineata*, (Cobcroft and Pankhurst, 2001). It is therefore possible that visual pigment lability is not restricted to species that inhabit variable-light environments.

5.4. Relocation of the Area Centralis During Ontogeny

The high densities of ganglion cells in specific regions of the vertebrate retina, the area centralis or visual streak, have been shown to provide high resolving power along specific visual axes and be related to the behavior or habitat of the animal (Hughes, 1977, 1985). In fishes, the area centralis is commonly found in

temporal or temporo-dorsal retina (Collin and Pettigrew, 1988a,b; Collin, 1999; Fig. 8.5). The development of an area centralis in fishes that have a continually growing retina has been addressed by Easter (1992) and, in the case of those species with a temporal area centralis, the visual axis is maintained by asymmetric growth of the retina. The mechanisms that control such growth involve differential cell addition (Cameron, 1995) and increased retinal stretching in nasal retina (Zygar et al., 1999).

Adult black bream possess an area centralis located in the dorso-temporal periphery when they feed from the substrate. However, it has been recently shown that during early larval and juvenile stages, when the fishes feed on plankton, the area centralis is located in a temporal position (Shand et al., 2000a,c). The change in the position of the area centralis takes place when the juveniles move to deeper water and begin feeding from the substrate (Fig. 8.9), although, in keeping with visual pigment changes, the timing can be variable (Shand et al., 2000c). The change from a temporal to a dorso-temporal location is mediated by cell death in central retina and differential cell addition at the retinal margins as the eye grows (Shand et al., 2000b). Such a change in the position of the area centralis and its maintenance in dorso-temporal retina is possible only because the retina is continuously growing.

6. Central Representation of Specialized Retinal Sampling

6.1. Tectal Magnification Factor

The high density of retinal ganglion cells associated with an area centralis, fovea, or horizontal streak may constitute a large proportion of the total population of ganglion cells in some species of fishes, despite occupying only a small proportion of the retinal area. Given the retinotopic organization of the optic tectum, does this specialized region of the retina occupy a disproportionately large region of the optic tectum? In the kelp bass *Paralabrax clathratus*, the foveal and perifoveal retinal regions

contain a ganglion cell density peak of 33.44×10^3 cells per mm^2 and subtend only $10\text{--}15^\circ$ of arc in the frontal visual field, but occupy a disproportionately large area (five times larger than a comparable region of the ventral or dorsal visual field) of the optic tectum (Schwassmann, 1968). Similarly, a magnified representation of a 25° -wide horizontal streak across the retinal meridian has been found in the optic tectum of the four-eyed fish, *Anableps microlepis* (Schwassmann and Kruger, 1965). In the lemon shark *Negaprion brevirostris*, the horizontal streak subtends 26% of the total visual field but the terminal fields of the axons from the ganglion cells comprising the streak occupy 52% of the tectal surface. The tectal magnification factor (number of microns on the tectal surface per degree of visual field coverage) in *N. brevirostris* is $100\mu\text{m}/^\circ$ within the visual streak and $33\mu\text{m}/^\circ$ outside the visual streak (Hueter, 1991). Qualitative comparisons between the optic tecta of species with comparably sized eyes with and without a visual streak also reveal that the optic tectum in species with a visual streak is appreciably larger (Ito and Murakami, 1984; Collin, 1987). Therefore, it has been suggested that the temporal area centralis projects to the thalamus and the visual streak projects to the optic tectum. Both anatomical and physiological investigations are still required to explore parallel processing in fishes.

6.2. Central Input of Binocular Information

In mammals, the partial decussation of retinal ganglion cell axons brings information from corresponding regions of the binocular visual fields into register. These axons then make accurate choices and synapse with target nuclei within the central nervous system. Both contra- and ipsilaterally projecting axons are essential for binocular vision where there is generally a direct relationship between the size of the binocular field and the region of the retina containing ipsilaterally projecting ganglion cells. Previous reports of bilateral visual projections in lampreys (De Miguel et al., 1990), cartilaginous fishes (Northcutt and Wathey, 1980;

Repérant et al., 1986; Northcutt, 1991), and early life history stages in bony fishes (Collin and Northcutt, 1991, 1995) has recently initiated a developmental study in the black bream *Acanthopagrus butcheri*, where a temporal area centralis "relocates" to a dorsal position during development (see Section 5.4; Fig. 8.9). In this model, temporal ganglion cells undergo a period of cell death and a new dorsal area centralis develops by the differential addition of new ganglion cells at the retinal margin (Shand et al., 2000b). Retro- and anterograde labeling studies confirm three sites in the optic tectum that receive ipsilateral input in small fishes. However, input to these retino-recipient tectal targets is progressively lost as the fish grows and the area centralis subtends different regions of the dorso-temporal hemifield (S.P. Collin, J. Shand, L.B.G. Tee, and L.D. Beazley, unpublished). The loss of input from a subset of temporal ganglion cells subtending the binocular visual field in *A. butcheri* constitute a transient ipsilateral projection and a putative switch in binocular processing. However, this needs to be confirmed physiologically, in addition to the anatomical and physiological substrates for binocular vision in adult fishes.

Acknowledgments. SPC is supported by an ARC Discovery Grant (DP0209452). JS is supported by the NHMRC (Australia) (Program Grant No. 993219). Nicole Thomas kindly helped with the preparation of Figures 8.4, 8.8, and 8.9.

References

- Ahlbert, I.-B. (1976). Organization of the cone cells in the retinae of salmon (*Salmo salar*) and trout (*Salmo trutta trutta*) in relation to their feeding habits. *Acta Zool.* 57:13-35.
- Ali, M.A., and Anctil, M.A. (1976). *Retinas of Fishes: An Atlas*. Berlin: Springer-Verlag.
- Anctil, M. (1969). Structure du rétine chez quelques téléostéens marin du plateau continental. *J. Fish. Res. Bd. Can.* 26:597-628.
- Anctil, M., and Ali, M.A. (1976). Cone droplets of mitochondrial origin in the retina of *Fundulus heteroclitus* (Pisces, Cyprinodontidae). *Zoomorphologie* 84:103-111.

- Arrese, C.A., Hart, N.S., Thomas, N., Beazley, L.D., and Shand, J. (2002). Trichromacy in Australian marsupials. *Curr. Biol.* 12:657-660.
- Avery, J.A., and Bowmaker, J.K. (1982). Visual pigments in the four-eyed fish *Anableps anableps*. *Nature* 298:62-64.
- Bathelt, D. (1970). Experimentelle und vergleichend morphologische Untersuchungen am visuellen System von Teleostiern. *Zool. Jb. Anat.* 87:402-470.
- Beatty, D.D. (1966). A study of the succession of visual pigments in Pacific salmon (*Oncorhynchus*). *Can. J. Zool.* 44:429-455.
- Beatty, D.D. (1975). Visual pigments of the American eel, *Anguilla rostrata*. *Vision Res.* 15:771-776.
- Beatty, D.D. (1984). Visual pigments and the labile scotopic visual system of fish. *Vision Res.* 24:1563-1573.
- Beaudet, L., and Hawryshyn, C.W. (1999). Ecological aspects of vertebrate visual ontogeny. In: *Adaptive Mechanisms in the Ecology of Vision* (Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., and Vallerga, S., eds.), pp. 383-412. Dordrecht: Kluwer.
- Beaudet, L., Browman, H.I., and Hawryshyn, C.W. (1993). Optic nerve response and retinal structure in rainbow trout of different sizes. *Vision Res.* 33:1739-1746.
- Beaudet, L., Novales Flamarique, I., and Hawryshyn, C.W. (1997). Cone photoreceptor topography in the retina of sexually mature pacific salmonid fishes. *J. Comp. Neurol.* 383:49-59.
- Berra, T.M., and Allen, G.R. (1989). Burrowing, emergence, behavior and functional morphology of the Australian salamanderfish, *Lepidogalaxias salamandroides*. *Fisheries* 14:2-10.
- Blaxter, J.H.S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.* 115:98-114.
- Boehlert, G.W. (1979). Retinal development in post-larval through juvenile *Sebastes diplopora*: Adaptation to a changing photic environment. *Rev. Can. Biol.* 38:265-280.
- Borwein, B., and Hollenberg, M.J. (1973). The photoreceptors of the "four-eyed" fish *Anableps anableps*, L. *J. Morphol.* 140:405-441.
- Bowmaker, J.K. (1990). Visual pigments of fishes. In: *The Visual System of Fish* (Douglas, R.H., and Djamgoz, M.B.A., eds.), pp. 81-107. London: Chapman & Hall.
- Bowmaker, J.K. (1991). The evolution of vertebrate visual pigments and photoreceptors. In: *Vision and Visual Dysfunction, Vol. 2* (Cronly-Dillon, J.R., and Gregory, R.L., eds.), pp. 63-81. Boca Raton: CRC Press.
- Bowmaker, J.K. (1995). The visual pigments of fish. *Prog. Retinal Eye Res.* 15:1-31.
- Bowmaker, J.K., and Kunz, Y.W. (1987). Ultraviolet receptors, tetrachromatic colour vision and retinal mosaics in the brown trout (*Salmo trutta*): Age-dependent changes. *Vision Res.* 27:2101-2108.
- Bowmaker, J.K., and Martin, G.R. (1985). Visual pigments and oil droplets in the penguin, *Spheniscus humboldti*. *J. Comp. Physiol. A.* 156:71-77.
- Boycott, B.B., and Wässle, H. (1974). The morphological types of ganglion cells of the domestic cat's retina. *J. Physiol. (Lond.)* 240:397-419.
- Bozzano, A., and Collin, S.P. (2000). Retinal ganglion cell topography in elasmobranchs. *Brain Behav. Evol.* 55:191-208.
- Braekevelt, C.R. (1973). Fine structure of the retinal pigment epithelium and photoreceptor cells of an Australian marsupial (*Setonix brachyurus*). *Can. J. Zool.* 51:1093-1100.
- Braekevelt, C.R. (1975). Photoreceptor fine structure in the northern pike (*Esox lucius*). *J. Fish Res. Bd. Can.* 32:1711-1721.
- Braekevelt, C.R. (1982). Photoreceptor fine structure in the goldeye (*Hiodon alosoides*) (Teleostei). *Anat. Embryol.* 165:177-192.
- Braekevelt, C.R. (1985). Photoreceptor fine structure in the archerfish (*Toxotes jaculatrix*). *Amer. J. Anat.* 173:89-98.
- Britt, L.L., Loew, E.R., and McFarland, W.N. (2001). Visual pigments in the early life history stages of Pacific northwest marine fishes. *J. Exp. Biol.* 204:2581-2587.
- Browman, H.I., and Hawryshyn, C.W. (1992). Thyroxine induces a precocial loss of ultraviolet photosensitivity in rainbow trout (*Oncorhynchus mykiss*, Teleostei). *Vision Res.* 32:2303-2312.
- Browman, H.I., Novales-Flamarique, I., and Hawryshyn, C.W. (1994). Ultraviolet photoreception contributes to prey search behavior in two species of zooplanktivorous fishes. *J. Exp. Biol.* 186:187-198.
- Butcher, E.O. (1938). The structure of the retina of *Fundulus heteroclitus* and the regions of the retina associated with the different chromatophoric responses. *J. Exp. Zool.* 79:275-293.
- Cameron, D.A. (1995). Asymmetric retinal growth in the adult teleost green sunfish (*Lepomis cyanellus*). *Visual Neurosci.* 12:95-102.
- Cameron, D.A., and Easter, S.S. Jr. (1993). The cone photoreceptor mosaic of the green sunfish (*Lepomis cyanellus*). *Visual Neurosci.* 10:375-384.
- Cameron, D.A., and Easter, S.S. (1995). Cone photoreceptor regeneration in adult fish retina: Phe-

- notopic determination and mosaic pattern formation. *J. Neurosci.* 15:2255–2271.
- Carleton, K.L., and Kocher T.D. (2001). Cone opsin genes of African cichlid fishes: Tuning spectral sensitivity by differential gene expression. *Mol. Biol. Evol.* 18:1540–1550.
- Carleton, K.L., Hárosi, F.I., and Kocher, T.D. (2000). Visual pigments of African cichlid fishes: Evidence for ultraviolet vision from microspectrophotometry and DNA sequences. *Vision Res.* 40:879–890.
- Carlisle, D.B., and Denton, E.J. (1959). On the metamorphosis of the visual pigments of *Anguilla anguilla* L. *J. Mar. Biol. Assoc. U.K.* 38:97–102.
- Chievitz, J.H. (1889). Untersuchungen über die Area centralis retinae. *Arch. Anat. Physiol. Anat. Abt. Suppl.* 1889:139–194.
- Chievitz, J.H. (1891). Ueber das Vorkommen der Area centralis retinae in den vier höheren Wirbelthierklassen. *Arch. Anat. Physiol. Anat. Abt.* 1891:311–333.
- Cobcroft, J.M., Pankhurst, P.M., Hart, P.R., and Battaglione, S.C. (2001). The effects of light intensity and algae-induced turbidity on feeding behaviour of larval striped trumpeter. *J. Fish. Biol.* 59:1181–1197.
- Collin, H.B., and Collin, S.P. (1988a). The cornea of the sandlance, *Limnichthyes fasciatus* (Creeiidae). *Cornea* 7(3):190–203.
- Collin, H.B., and Collin, S.P. (1996). Fine structure of the cornea in the freshwater salamanderfish, *Lepidogalaxias salamandroides*. *Cornea* 15:414–426.
- Collin, S.P. (1987). Retinal topography in reef teleosts. PhD thesis. University of Queensland, Australia.
- Collin, S.P. (1988). The retina of the shovel-nosed ray, *Rhinobatos batillum* (Rhinobatidae): Morphology and quantitative analysis of the ganglion, amacrine and bipolar cell populations. *Exp. Biol.* 47:195–207.
- Collin, S.P. (1989). Topography and morphology of retinal ganglion cells in the coral trout, *Plectropoma leopardus* (Serranidae): A retrograde cobaltous-lysine study. *J. Comp. Neurol.* 281:143–158.
- Collin, S.P. (1997). Specialisations of the teleost visual system: adaptive diversity from shallow-water to deep-sea. *Acta. Physiol. Scand.* 161 (Supplement 638):5–28.
- Collin, S.P. (1999). Behavioural ecology and retinal cell topography. In: *Adaptive Mechanisms in the Ecology of Vision* (Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., and Vallerga, S., eds.), pp. 509–535. Dordrecht: Kluwer Academic Publishers.
- Collin, S.P., and Ali, M.A. (1994). Multiple areas of acute vision in two freshwater teleosts, the creek chub, *Semotilus atromaculatus* (Mitchell) and the cutlips minnow, *Exoglossum maxillingua* (Lesueur). *Can. J. Zool.* 72:721–730.
- Collin, S.P., and Collin, H.B. (1988b). The morphology of the retina and lens of the sandlance *Limnichthyes fasciatus* (Creeiidae). *Exp. Biol.* 47:208–218.
- Collin, S.P., and Collin, H.B. (1988c). Topographic analysis of the retinal ganglion cell layer and the optic nerve in the sandlance, *Limnichthyes fasciatus* (Creeiidae, Perciformes). *J. Comp. Neurol.* 278:226–241.
- Collin, S.P., and Collin, H.B. (1993). The visual system of the Florida garfish, *Lepisosteus platyrhincus* (Ginglymodi). I. Retina. *Brain Behav. Evol.* 42:77–97.
- Collin, S.P., and Collin, H.B. (1998). Retinal and lenticular ultrastructure in the aestivating salamanderfish, *Lepidogalaxias salamandroides* (Galaxiidae, Teleostei) with special reference to a new type of photoreceptor mosaic. *Histol. Histopathol.* 13:1037–1048.
- Collin, S.P., and Collin, H.B. (1999). The foveal photoreceptor mosaic in the pipefish, *Corythoichthyes paxtoni* (Syngnathidae, Teleostei). *Histol. Histopathol.* 14:369–382.
- Collin, S.P., and Collin, H.B. (2001). The fish cornea: Adaptations for different aquatic environments. In: *Sensory Biology of Jawed Fishes: New Insights* (Kapoor, B.G., and Hara, T.J., eds.), pp. 57–96. Plymouth, UK: Science Publishers.
- Collin, S.P., and Northcutt, R.G. (1991). The development and evolution of ipsilateral projections in the retinofugal pathway of ray-finned fishes. *Invest. Ophthalmol. Vis. Sci.* 32:1033.
- Collin, S.P., and Northcutt, R.G. (1993). The visual system of the Florida garfish, *Lepisosteus platyrhincus* (Ginglymodi). III. Retinal ganglion cells. *Brain Behav. Evol.* 42:295–320.
- Collin, S.P., and Northcutt, R.G. (1995). The visual system of the Florida garfish, *Lepisosteus platyrhincus* (Ginglymodi). IV. Bilateral projections and the binocular visual field. *Brain Behav. Evol.* 45:34–53.
- Collin, S.P., and Pettigrew, J.D. (1988a). Retinal topography in reef teleosts. I. Some species with well-developed areae but poorly-developed streaks. *Brain Behav. Evol.* 31:269–282.
- Collin, S.P., and Pettigrew, J.D. (1988b). Retinal topography in reef teleosts. II. Some species with prominent horizontal streaks and high density areae. *Brain Behav. Evol.* 31:283–295.
- Collin, S.P., and Pettigrew, J.D. (1988c). Retinal ganglion cell topography in teleosts: A comparison

- between Nissl-stained material and retrograde labeling from the optic nerve. *J. Comp. Neurol.* 276:412-422.
- Collin, S.P., and Pettigrew, J.D. (1989). Quantitative comparison of the limits on visual spatial resolution set by the ganglion cell layer in twelve species of reef teleosts. *Brain Behav. Evol.* 34:184-192.
- Collin, S.P., and Potter, I.C. (2000). The ocular morphology of the southern hemisphere lamprey *Mordacia mordax* Richardson with special reference to a single class of photoreceptor and a retinal tapetum. *Brain Behav. Evol.* 55:120-138.
- Collin, S.P., Collin, H.B., and Ali, M.A. (1996). Ultrastructure and organization of the retina and pigment epithelium in the cutlips minnow, *Exoglossum maxillingua* (Cyprinidae, Teleostei). *Histol. Histopathol.* 11:55-69.
- Collin, S.P., Hoskins, R.V., and Partridge, J.C. (1997). Tubular eyes of deep-sea fishes: A comparative study of retinal topography. *Brain Behav. Evol.* 50:335-357.
- Collin, S.P., Hoskins, R.V., and Partridge, J.C. (1998). Seven retinal specializations in the tubular eye of the deep-sea pearleye, *Scopelarchus michaelisarsii*: A case study in visual optimization. *Brain Behav. Evol.* 51:291-314.
- Collin, S.P., Lloyd, D., and Wagner, H.-J. (2000). Visual and olfactory input to the CNS in foveate deep-sea teleosts: The relative importance of vision. *Phil. Trans. Roy. Soc. B.* 355:1315-1320.
- Collin, S.P., Lloyd, D.J., and Partridge, J.C. (1994). Retinal ganglion cell topography in deep-sea fishes: Intrafamilial variation within the family Alepocephalidae. *Proc. Aust. Neurosci. Soc.* 4:205.
- Collin, S.P., Potter, I.C., and Braekevelt, C.R. (1999). The ocular morphology of the Southern Hemisphere Lamprey *Geotria australis* Gray, with special reference to optical specializations and the characterization and phylogeny of photoreceptor types. *Brain Behav. Evol.* 54:96-118.
- Cook, J.E., and Becker, D.L. (1991). Regular mosaics of large displaced and non-displaced ganglion cells in the retina of a cichlid fish. *J. Comp. Neurol.* 306:668-684.
- Cook, J.E., and Chalupa, L.M. (2000). Retinal mosaics: New insights into an old concept. *TINS* 23:26-34.
- Cook, J.E., and Sharma, S.C. (1995). Large retinal ganglion cells in the channel catfish (*Ictalurus punctatus*): Three types with distinct dendritic stratification patterns form similar but independent mosaics. *J. Comp. Neurol.* 362:331-349.
- Cook, J.E., Becker, D.L., and Kapila, R. (1992). Independent mosaics of large inner- and outer-stratified ganglion cells in the goldfish retina. *J. Comp. Neurol.* 318:355-366.
- Cook, J.E., Kondrashev, S.L., and Pudugolnikova, T.A. (1996). Biplexiform ganglion cells, characterized by dendrites in both outer and inner plexiform layers, are regular, mosaic forming elements of teleost fish retinae. *Visual Neurosci.* 13:517-528.
- Cook, J.E., Pudugolnikova, T.A., and Kondrashev, S.L. (1999). Species-dependent variation in the dendritic stratification of apparently homologous retinal ganglion cell mosaics in two neoteleost fishes. *Vision Res.* 39:2615-2631.
- Crescitelli, F. (1956). The nature of the lamprey visual pigment. *J. Gen. Physiol.* 39:423-435.
- Dartnall, H.J.A., and Lythgoe, J.N. (1965). The spectral clustering of visual pigments. *Vision Res.* 5:81-100.
- De Miguel, E., Rodicio, M.C., and Anadon, R. (1990). Organization of the visual system in larval lampreys: An HRP study. *J. Comp. Neurol.* 302:529-542.
- Denton, E.J., and Locket, N.A. (1989). Possible wavelength discrimination by multibank retinae in deep-sea fishes. *J. Mar. Biol. Assoc. U.K.* 69:409-435.
- Deutschlander, M.E., Greaves, D.K., Haimberger, T.J., and Hawryshyn, C.W. (2001). Functional mapping of ultraviolet photosensitivity during metamorphic transitions in a salmonid fish, *Oncorhynchus mykiss*. *J. Exp. Biol.* 204:2401-2413.
- Douglas, R.H., Collin, S.P., and Corrigan, J. (2002). The eyes of suckermouth armoured catfish (Loricariidae, subfamily Hypostomus): pupil response, lenticular longitudinal spherical aberration and retinal topography. *J. Exp. Biol.* 205:3425-3433.
- Douglas, R.H., Harper, R.D., and Case, J.F. (1998a). The pupil response of a teleost fish, *Porichthys notatus*: A description and comparison to other species. *Vision Res.* 38:2697-2710.
- Douglas, R.H., Partridge, J.C., and Marshall, N.J. (1998b). The eyes of deep-sea fish. I. Lens pigmentation, tapeta and visual pigments. *Prog. Retinal Eye Res.* 17:587-636.
- Dunn-Meynell, A.A., and Sharma, S.C. (1986). The visual system of the channel catfish (*Ictalurus punctatus*). I. Retinal ganglion cell morphology. *J. Comp. Neurol.* 247:32-55.
- Easter, S.S. Jr. (1992). Retinal growth in foveated teleosts: Nasotemporal asymmetry keeps the fovea in temporal retina. *J. Neurosci.* 12:2381-2392.
- Eberle, H. (1967). Cone length and chromatic aberration in *Lebistes reticulatus*. *Z. Verlg. Physiol.* 57:172-173.
- Engström, K. (1960). Cone types and cone arrangements in the retina of some cyprinids. *Acta Zool.* 41:277-295.

- Engström, K. (1963a). Cone types and cone arrangements in teleost retinæ. *Acta Zool. (Stockh.)* 44:179–243.
- Engström, K. (1963b). Structure, organization and ultrastructure of the visual cells in the teleost family Labridae. *Acta Zool. (Stockh.)* 44:1–41.
- Evans, B.I., and Fernald, R.D. (1993). Retinal transformation at metamorphosis in the winter flounder (*Pseudopleuronectes americanus*). *Visual Neurosci.* 10:1055–1064.
- Evans, B.I., Harosi, F.I., and Fernald, R.D. (1993). Photoreceptor spectral absorbance in larval and adult winter flounder (*Pseudopleuronectes americanus*). *Visual Neurosci.* 10:1065–1071.
- Fernald, R.D. (1988). Aquatic adaptations in fish eyes. In: *Sensory Biology of Aquatic Animals* (Atema, J., Fay, R.R., Popper, A.N., and Tavolga, W.N., eds.), pp. 435–466. New York: Springer-Verlag.
- Fineran, B.A., and Nicol, J.A.C. (1974). Studies on the eyes of New Zealand parrot-fishes (Labridae). *Proc. Roy. Soc. (Lond.) B.* 186:217–247.
- Franz, V. (1932). Auge und Akkommodation von *Petromyzon (Lampetra) fluviatilis*, L. *Zool. Jb. (Zool.)* 52:118–178.
- Fritsches, K.A., and Marshall, N.J. (2002). Independent conjugate eye movements during optokinetic in teleost fish. *J. Exp. Biol.* 205:1241–1252.
- Fritsches, K.A., and Marshall, J. (1999). A new category of eye movements in a small fish. *Curr. Biol.* 9:R272–R273.
- Fritsches, K.A., Partridge, J.C., Pettigrew, J.D., and Marshall, N.J. (2000). Colour vision in billfish. *Phil. Trans. R. Soc. (Lond.) B.* 355:1253–1256.
- Fritsch, B., and Collin, S.P. (1990). Dendritic distribution of two populations of ganglion cells and the retinopetal fibres in the retina of the silver lamprey (*Ichthyomyzon unicuspis*). *Visual Neurosci.* 4:533–545.
- Fröhlich, E., and Wagner, H.-J. (1998). Development of multibank rod retinæ in deep-sea fishes. *Visual Neurosci.* 15:1–7.
- Fuiman, L.A., and Delbos, B.C. (1998). Developmental changes in visual sensitivity of red drum, *Sciaenops ocellatus*. *Copeia* 1998:936–943.
- Govardovskii, V.I., Rohlich, P., Szel, A., and Zueva, L.V. (1992). Immunocytochemical reactivity of rod and cone visual pigments in the sturgeon retina. *Visual Neurosci.* 8:531–537.
- Harkness, L., and Bennett-Clarke, H.C. (1978). The deep fovea as a focus indicator. *Nature Lond.* 272:814–816.
- Hart, N.S., Partridge, J.C., and Cuthill, I.C. (1998). Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). *J. Exp. Biol.* 201:1433–1446.
- Hawryshyn, C.W., Arnold, M.G., Chaisson, D.J., and Martin, P.C. (1989). The ontogeny of ultraviolet sensitivity in rainbow trout (*Salmo gairdneri*). *Visual Neurosci.* 2:247–254.
- Hayes, B.P., Martin, G.R., and Brooke, M. de L. (1991). Novel area serving binocular vision in the retinæ of procellariform seabirds. *Brain Behav. Evol.* 37:79–84.
- Helvick, J.V., Drivenes, O., Harboe, T., and Seo, H.-C. (2001). Topography of different photoreceptor cell types in the larval retinæ of Atlantic halibut (*Hippoglossus hippoglossus*). *J. Exp. Biol.* 204:2553–2559.
- Hisatomi, O., Satoh, T., and Tokunaga, F. (1997). The primary structure and distribution of killifish visual pigments. *Vision Res.* 37:3089–3096.
- Hitchcock, P.F., and Easter, S.S. Jr. (1986). Retinal ganglion cells in goldfish: A qualitative classification into four morphological types, and a quantitative study of the development of one of them. *J. Neurosci.* 6:1037–1050.
- Hueter, R.E. (1991). Adaptations for spatial vision in sharks. *J. Exp. Zool. Suppl.* 5:130–141.
- Hughes, A. (1977). The topography of vision in mammals of contrasting life style: Comparative optics and retinal organisation. In: *Handbook of Sensory Physiology, Vol. VII/5* (Crescitelli, F., ed.), pp. 613–756. Berlin: Springer Verlag.
- Hughes, A. (1985). New perspectives in retinal organization. In: *Progress in Retinal Research, Vol. 4* (Osbourne, N.N., and Chader, G.J., eds.), pp. 243–313. Oxford: Pergamon.
- Ishikawa, M., Hashimoto, Y., Tonosaki, A., and Sakuragi, S. (1997). Preference of peanut agglutinin labeling for long wavelength sensitive cone photoreceptors in the dace retina. *Vision Res.* 37:383–387.
- Ito, H., and Murakami, T. (1984). Retinal ganglion cells in two teleost species, *Sebastes marmoratus* and *Navodon modestus*. *J. Comp. Neurol.* 229:80–96.
- Job, S.D., and Bellwood, D.R. (1996). Visual acuity and feeding in larval *Premnas biaculeatus*. *J. Fish Biol.* 48:952–963.
- Job, S., and Bellwood, D. (2000). Light sensitivity in larval fishes: implications for vertical zonation in the pelagic zone. *Limnol. Oceanog.* 45:362–371.
- Job, S., and Shand, J. (2001). Spectral sensitivity of larval and juvenile coral reef fishes: Implications for feeding in a variable light environment. *Marine Ecol. Prog. Ser.* 214:267–277.

- Johns, P.A. (1977). Growth of the adult goldfish eye. III. Source of the new retinal cells. *J. Comp. Neurol.* 176:343-358.
- Johns, P.A., and Easter, S.S. Jr. (1977). Growth of the adult goldfish eye. II. Increase in retinal cell number. *J. Comp. Neurol.* 176:331-342.
- Kahmann, H. (1934). Über das Vorkommen einer Fovea centralis im Knochenfischeauge. *Zool. Anz.* 106:49-55.
- Kirschfeld, K. (1976). The resolution of lens and compound eyes. In: *Neural Principles in Vision* (Zettler, F., and Weiler, R., eds.), pp. 354-370. Berlin: Springer-Verlag.
- Kolb, H., and Jones, J. (1987). The distinction by light and electron microscopy of two types of cone containing colourless oil droplets in the retina of the turtle. *Vision Res.* 27:1445-1458.
- Kunz, Y.W., Shuilleabhain, M.N., and Callaghan, E. (1985). The eye of the venomous marine teleost *Trachinus vipera* with special reference to the structure and ultrastructure of visual cells and pigment epithelium. *Exp. Biol.* 43:161-178.
- Land, M.F. (1981). Optics and vision in invertebrates. In: *Handbook of Sensory Physiology, Vol. VII/6B: Vision in Invertebrates* (Autrum, H., ed.), pp. 471-592. Berlin: Springer-Verlag.
- Land, M.F. (1999). Visual optics: The sandlance eye breaks all the rules. *Curr. Biol.* 9:R286-R288.
- Lasater, E.M. (1982). Spatial receptive fields of catfish retinal ganglion cells. *J. Neurophysiol.* 48:823-825.
- Levine, J.S., and MacNichol, E.F. (1979). Visual pigments in teleost fishes: Effects of habitat, microhabitat and behaviour on visual system evolution. *Sensory Process.* 3:95-131.
- Locket, N.A. (1970). Deep-sea fish retinas. *British Med. Bull.* 26:107-111.
- Locket, N.A. (1985). The multiple bank fovea of *Bajacalifornia drakei*, an alepocephalid deep-sea teleost. *Proc. Roy. Soc. (Lond.) B.* 224:7-22.
- Locket, N.A. (1992). Problems of deep foveas. *Aust. New Zeal. J. Ophthalmol.* 20:281-295.
- Loew, E.R. (1995). Determinants of visual pigment spectral location and photoreceptor cell spectral sensitivity. In: *Neurobiology and Clinical Aspects of the Outer Retina* (Djamgoz, M.B.A., Archer, S.N., and Vallerger, S., eds.), pp. 57-77. London: Chapman & Hall.
- Loew, E.R., and Sillman, A.J. (1993). Age-related changes in the visual pigments of the white sturgeon (*Acipenser transmontanus*). *Can. J. Zool.* 71:1552-1557.
- Loew, E.R., and Wahl, C.M. (1991). A short-wavelength sensitive cone mechanism in juvenile yellow perch, *Perca flavescens*. *Vision Res.* 31:353-360.
- Loew, E.R., McFarland, W.N., Mills, E.L., and Hunter, D. (1993). A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Can. J. Zool.* 71:384-386.
- Lyll, A.H. (1956). Occurrence of triple and quadruple cones in the retina of the minnow (*Phoxinus laevis*). *Nature* 177:1086-1087.
- Lyll, A.H. (1957a). Cone arrangements in teleost retinæ. *Q. J. Microsc. Sci.* 98:189-201.
- Lyll, A.H. (1957b). The growth of the trout retina. *Q. J. Microsc. Sci.* 98:101-110.
- Lythgoe, J.N. (1979). *The Ecology of Vision*. Oxford: Oxford University Press.
- Lythgoe, J.N. (1984). Visual pigments and environmental light. *Vision Res.* 24:1539-1550.
- Lythgoe, J.N., and Partridge, J.C. (1989). Visual pigments and the acquisition of visual information. *J. Exp. Biol.* 146:1-20.
- Lythgoe, J.N., and Partridge, J.C. (1991). The modelling of optimal visual pigments of dichromatic teleosts in green coastal waters. *Vision Res.* 31:361-371.
- MacNichol, E.F., Kunz, Y.W., Levine, J.S., Harosi, F.I., and Collins, B.A. (1978). Ellipsosomes: Organelles containing a cytochrome-like pigment in the retinal cones of certain fishes. *Science* 200:549-552.
- Marc, R.E., and Sperling, H.G. (1976). The chromatic organization of the goldfish retina. *Vision Res.* 16:1211-1224.
- McCormick, M.I. (1993). Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula* (Family: Mullidae). *Environ. Biol. Fish.* 37:269-282.
- McEwan, M.R. (1938). A comparison of the retina of the Mormyrids with that of various other teleosts. *Acta Zool.* 19:427-465.
- McFarland, W.N., and Loew, E.R. (1994). Ultraviolet visual pigments in marine fishes of the Family Pomacentridae. *Vision Res.* 34:1393-1396.
- Mednick, A.S., and Springer, A.D. (1988). Asymmetric distribution of retinal ganglion cells in goldfish. *J. Comp. Neurol.* 268:49-59.
- Mednick, A.S., Berk, M.F., and Springer A.D. (1988). Asymmetric distribution of cells in the inner nuclear and cone mosaic layers of the goldfish retina. *Neurosci. Letts.* 94:241-246.
- Munk, O. (1968). The eyes of *Amia* and *Lepisosteus* (Pisces, Holostei) compared with the brachiopterygian and teleostean eyes. *Vidensk Meddr. Dansk. Naturh. Foren.* 131:109-127.

- Munk, O. (1970). On the occurrence and significance of horizontal band-shaped retinal areas in teleosts. *Vidensk Meddr. Dansk Naturh. Foren.* 133:85–120.
- Munk, O. (1975). On the eyes of two foveate notosudid teleosts, *Scopelosaurus hoedti* and *Ahliesaurus berryi*. *Vidensk Meddr. Dansk Naturh. Foren.* 138:87–125.
- Munk, O. (1990). Changes in the visual cell layer of the duplex retina during growth of the eye of a deep-sea teleost *Gempylus serpens* Cuvier 1829. *Acta Zool.* 71:89–95.
- Muntz, W.R.A., and Mouat, G.S.V. (1984). Annual variations in the visual pigments of brown trout inhabiting lochs providing different light environments. *Vision Res.* 24:1575–1580.
- Nag, T.C. (1995). Ultrastructure of ellipsosomes in the retina of *Garra lamta*. *J. Electron Microsc.* 44:405–407.
- Nag, T.C., and Bhattacharjee, J. (1989). Retinal organisation in a hill stream cyprinid, *Crossocheilus latius latius* Hamilton. *Exp. Biol.* 48:197–202.
- Nag, T.C., and Bhattacharjee, J. (1995). Retinal ellipsosomes: Morphology, development, identification, and comparison with oil droplets. *Cell. Tiss. Res.* 279:633–637.
- Naka, K.-I., and Carraway, N.R.G. (1975). Morphological and functional identification of catfish retinal neurons. I. Classical morphology. *J. Neurophysiol.* 38:53–71.
- Nicol, J.A.C. (1989). *The Eyes of Fishes*. Oxford: Clarendon Press.
- Northcutt, R.G. (1991). Visual pathways in elasmobranchs: organisation and phylogenetic implications. *J. Exp. Zool. Suppl.* 5:97–107.
- Northcutt, R.G., and Wathey, J.C. (1980). Guitarfish possess ipsilateral as well as contralateral retinofugal projections. *Neurosci. Letts.* 20:237–242.
- Novales-Flamarique, I. (2001). Gradual and partial loss of corner cone-occupied area in the retina of rainbow trout. *Vision Res.* 41:3073–3082.
- Novales-Flamarique, I., and Browman, H.I. (2001). Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynchus mykiss*) under polarised light. *J. Exp. Biol.* 204:2415–2422.
- Novales-Flamarique, I., and Hárosi, F.I. (2000). Photoreceptors, visual pigments, and ellipsosomes in the killifish, *Fundulus heteroclitus*: A microspectrophotometric and histological study. *Visual Neurosci.* 17:403–420.
- Novales-Flamarique, I., and Hawryshyn, C.W. (1998). Photoreceptor types and their relation to the spectral and polarization sensitivities of clupeid fishes. *J. Comp. Physiol. A.* 182:793–803.
- O'Day, K. (1938). The visual cells of the platypus (*Ornithorhincus*). *Brit. J. Ophthalmol.* 22:321–328.
- Ohtsuka, T. (1985). Relation of spectral types to oil droplets in cones of turtle retina. *Science* 229:874–877.
- Pankhurst, N.W. (1982). Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). *J. Fish. Biol.* 21:127–140.
- Pankhurst, P.M., and Hilder, P.E. (1998). Effect of light intensity on feeding of striped trumpeter *Latris lineata* larvae. *Mar. Fresh. Res.* 49:363–368.
- Pankhurst, P.M., Pankhurst, N.W., and Montgomery, J.C. (1993). Comparison of behavioural and morphological measures of visual acuity during ontogeny in a teleost fish, *Forsterygion varium*, Tripterygiidae (Forster, 1801). *Brain Behav. Evol.* 42:178–88.
- Parry, J.W.L., and Bowmaker, J.K. (2000). Visual pigment reconstitution in intact goldfish retina using synthetic retinaldehyde isomers. *Vision Res.* 40:2241–2247.
- Partridge, J.C. (1989). The visual ecology of avian cone oil droplets. *J. Comp. Physiol. A.* 165:415–426.
- Partridge, J.C., and Cummings, M.E. (1999). Adaptation of visual pigments to the aquatic environment. In: *Adaptive Mechanisms in the Ecology of Vision* (Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., and Vallergera, S., eds.), pp. 251–283. Dordrecht: Kluwer Academic Publishers.
- Partridge, J.C., Archer, S.N., and van Oostrum, J. (1992). Single and multiple visual pigments in deep-sea fishes. *J. Mar. Biol. Assoc. U.K.* 72: 113–130.
- Pedler, C., and Tilly, R. (1964). The nature of the gecko visual cells: A light and electron microscopic study. *Vision Res.* 4:499–510.
- Pettigrew, J.D., and Collin, S.P. (1995). Terrestrial optics in an aquatic eye: The sandlance, *Limnichthyes fasciatus* (Creediidae, Teleostei). *J. Comp. Physiol. A.* 177:397–408.
- Pettigrew, J.D., Collin, S.P., and Fritsches, K. (2000). Prey capture and accommodation in the sandlance, *Limnichthyes fasciatus* (Creediidae, Teleostei). *J. Comp. Physiol. A.* 186:247–260.
- Poling, K.R., and Fuiman, L.A. (1997). Sensory development and concurrent behavioural changes in Atlantic croaker larvae. *J. Fish Biol.* 51:402–421.
- Pumphrey, R.J. (1948). The theory of the fovea. *J. Exp. Biol.* 25:299–312.
- Raymond, P.A. (1995). Development and organization of photoreceptors. In: *Neurobiology and Clinical Aspects of the Outer Retina* (Djamgoz, M.B.A., Archer, S.N., and Vallergera, S., eds.), pp. 1–23. London: Chapman and Hall.

- Reckel, F., Melzer, R.R., and Smola, U. (2001). Outer retinal fine structure of the garfish *Belone belone* (L.) (Belonidae, Teleostei) during light and dark adaptation: Photoreceptors, cone patterns and densities. *Acta Zool. (Stockh.)* 82:89–105.
- Repérant, J., Miceli, D., Rio, J.P., Peyrichoux, J., Pierre, J., and Kipitchnikova, E. (1986). The anatomical organization of retinal projections in the shark *Scyliorhinus canicula* with special reference to the evolution of the selachian primary visual system. *Brain Res. Rev.* 11:227–248.
- Robinson, S.R. (1994). Early vertebrate colour vision. *Nature* 367:121.
- Saidel, W.M. (1987). An usual optic fiber pattern in the retina of the primitive fish *Pantodon buchholzi*, Peters. *Vision Res.* 27:511–516.
- Saidel, W.M. (2000). Coherence in nervous system design: the visual system of *Pantodon buchholzi*. *Phil. Trans. Roy. Soc. (Lond.) B.* 355:1177–1181.
- Saidel, W.M., and Fabiane, R.S. (1998). Optomotor response of *Anableps anableps* depends on the field of view. *Vision Res.* 38:2001–2008.
- Sakai, H.M., Naka K.-I., and Dowling, J.E. (1986). Ganglion cell dendrites are presynaptic in catfish retina. *Nature* 319:495–497.
- Scholes, J.H. (1975). Colour receptors and the synaptic connexions in the retina of a cyprinid fish. *Phil. Trans. Roy. Soc. (Lond.) B.* 270:61–118.
- Schwartz, E. (1971). Ein septum papillaris im Auge von *Pantodon buchholzi* Pet. (Teleostei, Osteoglossiformes). *Zeitsch. für Morph. der Tiere* 70:119–127.
- Schwassmann, H.O. (1968). Visual projection upon the optic tectum in foveate marine teleosts. *Vision Res.* 8:1337–1348.
- Schwassmann, H.O., and Kruger, L. (1965). Experimental analysis of the visual system of the four-eyed fish *Anableps microlepis*. *Vision Res.* 5:269–281.
- Shamim, K.M., Tóth, P., and Cook, J.E. (1997). Large retinal ganglion cells in the pipid frog *Xenopus laevis* form independent, regular mosaics resembling those of teleost fish. *Vis. Neurosci.* 14: 811–826.
- Shand, J. (1993). Changes in the spectral absorption of cone visual pigments during settlement of the goatfish *Upeneus tragula*: The loss of red sensitivity as a benthic existence begins. *J. Comp. Physiol. A.* 173:115–121.
- Shand, J. (1994). Changes in retinal structure during development and settlement of the goatfish *Upeneus tragula*. *Brain Behav. Evol.* 43:51–60.
- Shand, J. (1997). Ontogenetic changes in retinal structure and visual acuity: A comparative study of coral-reef teleosts with differing post-settlement lifestyles. *Environ. Biol. Fish.* 49:307–322.
- Shand, J., Archer, M.A., and Collin, S.P. (1999). Ontogenetic changes in the retinal photoreceptor mosaic in a fish, the black bream, *Acanthopagrus butcheri*. *J. Comp. Neurol.* 412:203–217.
- Shand, J., Archer, M.A., Thomas, N., and Cleary, J. (2001a). Retinal development of West Australian dhufish, *Glaucosoma hebraicum*. *Visual Neurosci.* 18:711–724.
- Shand, J., Chin, S.M., Harman, A.M., and Collin, S.P. (2000a). The relationship between the position of the area centralis and feeding behaviour in juvenile black bream *Acanthopagrus butcheri* (Sparidae:Teleostei). *Phil. Trans. Roy. Soc. (Lond.) B.* 355:1183–1186.
- Shand, J., Chin, S.M., Harman, A.M., and Collin, S.P. (2000b). Mechanisms for changing the position of the area centralis in a retina that undergoes continual growth. *Proc. Aust. Neurosci. Soc.* 11:100.
- Shand, J., Chin, S.M., Harman, A.M., Moore, S., and Collin, S.P. (2000c). Variability in the location of the retinal ganglion cell area centralis is correlated with ontogenetic changes in feeding behaviour in the black bream, *Acanthopagrus butcheri* (Sparidae, Teleostei). *Brain Behav. Evol.* 55:176–190.
- Shand, J., Hart, N.S., Thomas, N., and Partridge, J.C. (2002). Developmental changes in the cone visual pigments of black bream *Acanthopagrus butcheri*. *J. Exp. Biol.* (in press).
- Shand, J., Partridge, J.C., Archer, S.N., Potts, G.W., and Lythgoe, J.N. (1988). Spectral absorbance changes in the violet/blue sensitive cones of the juvenile pollack, *Pollachius pollachius*. *J. Comp. Physiol. A.* 163:699–703.
- Sivak, J.G. (1976). Optics of the eye of the “four-eyed” fish (*Anableps anableps*). *Vision Res.* 16: 531–534.
- Sivak, J.G. (1988). Optics of amphibious eyes in vertebrates. In: *Sensory Biology of Aquatic Animals* (Atema, J., Fay, R.R., Popper, A.N., and Tavolga, W.N., eds.). pp. 467–485. New York: Springer-Verlag.
- Sivak, J.G., and Warburg, M.R. (1983). Changes in the optical properties of the eye during metamorphosis of an anuran, *Pleobates syriacus*. *J. Comp. Physiol.* 150:329–332.
- Slonaker, J.R. (1897). A comparative study of the area of acute vision in vertebrates. *J. Morphol.* 13:445–492.
- Snyder, A.W., and Miller, W.H. (1978). Telephoto lens system of falconiform eyes. *Nature Lond.* 275:127–129.

- Steenstrup, S., and Munk, O. (1980). Optical function of the convexiculate fovea with special regard to notosudid deep-sea teleosts. *Optica Acta* 27: 949-964.
- Takei, S., and Somiya, H. (2001). Guanine-type retinal tapetum and ganglion cell topography in the retina of a carangid fish, *Kaiwarinus equula*. *Proc. Roy. Soc. (Lond.) B* 269:75-82.
- Uemura, M., Somiya, H., Moku, M., and Kawaguchi, K. (2000). Temporal and mosaic distribution of large cells in the retina of a daggertooth aulopiform deep-sea fish (*Anopterus pharao*). *Phil. Trans. Roy. Soc. (Lond.) B* 355:1161-1166.
- van der Meer, H.J. (1994). Ontogenetic change of visual thresholds in the cichlid fish *Haplochromis sauvagei*. *Brain Behav. Evol.* 44:40-49.
- Vilter, V. (1954). Différenciation fovéale dans l'appareil visuel d'un poisson abyssal, le Bathylage benedicti. *Société de Biol.* 148:59-63.
- Wagner, H.-J. (1990). Retinal structure of fishes. In: *The Visual System of Fish* (Douglas, R.H., and Djamgoz, M.B.A., eds.), pp. 109-157. London: Chapman and Hall.
- Wagner, H.-J., Fröhlich, E., Negishi, K., and Collin, S.P. (1998). The eyes of deep-sea fishes. II. Functional morphology of the retina. *Prog. Retinal Eye Res.* 17:637-685.
- Wagner, H.-J., Menezes, N.A., and Ali, M.A. (1976). Retinal adaptations in some Brazilian tide pools fishes (Teleostei). *Zoomorphol.* 83:209-226.
- Wald, G. (1939). On the distribution of vitamin A₁ and A₂. *J. Gen. Physiol.* 22:391-415.
- Wald, G. (1958). The significance of vertebrate metamorphosis. *Science* 128:1481-1490.
- Walls, G.L. (1937). Significance of the foveal depression. *Arch. Ophthalmol.* 18:912-919.
- Walls, G.L. (1940). Postscript on image expansion by the foveal clivus. *Arch. Ophthalmol.* 23:831-832.
- Walls, G.L. (1942). *The Vertebrate Eye and Its Adaptive Radiation*. Michigan: Cranbrook Institute of Science.
- Wässle, H., Peichl, L., and Boycott, B.B. (1981). Morphology and topography of on- and off-alpha cells in the cat retina. *Proc. Roy. Soc. (Lond.) B* 212:157-175.
- Whitmore, A.V., and Bowmaker, J.K. (1989). Seasonal variation in cone sensitivity and short-wave absorbing visual pigments in the rudd *Scardinius erythrophthalmus*. *J. Comp. Physiol. A* 166: 103-115.
- Wong, R.O.L. (1989). Morphology and distribution of neurons in the retina of the American garter snake *Thamnophis sirtalis*. *J. Comp. Neurol.* 283: 587-601.
- Wood, P., and Partridge, J.C. (1993). Opsin substitution induced in retinal rods of the eel (*Anguilla anguilla* (L.): A model for G-protein-linked receptors. *Proc. Roy. Soc. (Lond.) B* 254:227-232.
- Wood, P., Partridge, J.C., and De Grip, W.J. (1992). Rod visual pigment changes in the elver of the eel *Anguilla anguilla*, L. measured by microspectrophotometry. *J. Fish Biol.* 41:601-611.
- Yew, D.T., Chan, Y.W., Lee, M., and Lam, S. (1984). A biophysical, morphological and morphometrical survey of the eye of the small shark (*Hemiscyllium plagiosum*). *Anat. Anz.* 155:355-363.
- Yokoyama, S. (1997). Molecular genetic basis of adaptive selection: Examples from color vision in vertebrates. *Ann. Rev. Genet.* 31:315-316.
- Young, R.W., and Martin, G.R. (1984). Optics of retinal oil droplets: a model of light collection and polarization detection in the avian retina. *Vision Res.* 24:129-137.
- Zaunreiter, M., Junger, H., and Kotschal, K. (1991). Retinal morphology of cyprinid fishes: A quantitative histological study of ontogenetic changes and interspecific variation. *Vision Res.* 31:383-394.
- Zygar, C.A., Lee, M.J., and Fernald R.D. (1999). Nasotemporal asymmetry during teleost retinal growth: Preserving an area of specialization. *J. Neurobiol.* 41:435-442.