

Variation in the Development of the Fish Retina

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Abstract.—Although the basic structure of the vertebrate retina is similar across taxa, high variability in specific features of the fish retina reflects the differences in visual microhabitat of these species. The vertebrate retina is the first step in the neural integration of visual information. A great deal of retinal function can be inferred from structure, and as these relationships continue to be revealed, we are gaining new insights into how vision is integrated by the nervous system. Among fishes, the developmental rate and acquisition of retinal structures is highly variable. While some species develop all structures early in embryogenesis, others delay acquisition of the full adult retinal complement of cells until months after hatching. Given the tight relationship between structure and function, differences in the timing of retinogenesis have implications for the vision-based survival skills of the early life history stages and for the overall ecology and fitness of the species. Although much of the observed variation may be related to altricial versus precocial life history strategies, we suggest that protracted retinal development also reflects and separates the constraints imposed by the requirements of foraging and predator avoidance. As evidenced by a typically monochromatic all-cone retina, the eye of early fish larvae is adapted for efficient foraging in bright light. At later stages, an improved ability to identify the presence of predators is acquired via addition of rod photoreceptors for low light vision, as well as multiple cone spectral channels (and regularly geometric cone mosaics) for increased contrast and motion sensitivity. The larval retina of some species exhibits further specializations, such as the pure rod retina of the eel *leptocephalus* and the pure green cone retina of many marine teleosts. Overall, variation in the development of the teleost retina can be viewed as a continuum from very rapid to greatly delayed. The developmental trajectory of the visual system in any given species represents a product of evolutionary history, developmental constraints, and foraging and predation pressures.

Introduction

Vision, in its simplest form, allows organisms to locate prey and detect predators (among other things). Visual capabilities are largely determined by the structure and function of the neural retina. Thus, for species in which vision plays a central role, the time course of retinal neural development should be a good indicator of the strength of selective pressures for the detection of predators and prey during the early life history. Following from these underlying premises, the goal of this paper is to develop a framework to identify the key selective pressures that are correlated with

the timing of retinal development in teleost fishes. The paper is directed towards describing and explaining the underlying variability in development of the teleost visual system, both intra- and interspecifically. In particular, we evaluate whether the development of vision is an ontogenetically programmed event, strongly tied to reproductive strategy, or whether the observed variation in sensory development occurs in response to ecological pressures. The structure and function of the fish (and vertebrate) retina, the typical developmental sequence of rod and cone photoreceptors, and the expression of photopigments are all reviewed. Several aspects of cell

patterning in the teleost retina (cone mosaics and receptive field organization) are related to the functioning of the eye. Finally, the variation in the sequence of visual development among fishes is linked to constraints on larval survival.

Sensory systems in newborn animals, and the behaviors based upon the information that they supply, develop along a pattern that is both genetically and environmentally determined (e.g., Scott 1962; Blakemore 1977; Hirsch and Leventhal 1978; Bateson 1981; Immelmann and Suomi 1981; Eysel et al. 1985; Mimura 1986; Browman 1989; Pigliucci 2001; Kroger et al. 2003). Few studies address the relationship between acquisition of behavioral repertoires and the structural and functional development of the sensory systems upon which they are based (though many have examined these two processes independently). Variation in the developmental timetable may be regulated by the organism's genome and developmental history (Lewis 1991) or produced by selective pressures from foraging and predator avoidance (Blaxter 1986). Regulation of visual system development is most likely a combination of these proximate and ultimate influences, allowing selection for successful ecological function (*sensu* Mayr 1982).

Among fishes, the developmental timetable of organ systems is related to whether the species' reproductive/life history strategy is precocial or altricial (Balon 1986, 2001, 2002). Precocial species allocate a large amount of resources to a small number of eggs, and the young hatch at an advanced stage of development (Balon 1981). This is analogous to K-selection (MacArthur and Wilson 1967; Ayala 1968) or Hutchinson's (1978) prudent reproductive strategy. At the other end of the spectrum, altricial species allocate far fewer resources to each gamete, releasing a large number of small eggs that hatch at a less developed stage (Balon 2001, 2002). Altricial larvae accumulate energy resources until they reach a sufficient size to complete development, usually in a metamorphic transformation. Altricial reproduction is also termed r-selection (MacArthur and Wilson 1967; Ayala 1968) or a prodigal strategy (Hutchinson 1978). These two extremes delimit a gradient of species-specific developmental strategies. Along this gradient, parental investment of energy in each egg determines (to a large, but not complete, extent) the stage of development at which the young hatch, as well as their individual chances of survival (Sinervo and McEdward 1988).

Matsuda (1987) suggested two developmental processes that may be involved in evolution: embryonization and variation in hatching time (Figures 1 and 2). Embryonization is a decrease in developmental time resulting in the loss of the larval period. This foreshortening of the developmental trajectory underlies the trend from the indirect to the direct life history pattern. Indirectly developing species possess a larval period. Directly developing species do not, and developmental events, culminating in the juvenile form, occur during the embryonic period (Figure 2). Hatching time varies considerably in fish. Hatching occurs early in altricial species, such that they exit the egg in an undeveloped state (extreme case: no retinal pigment, pectoral fin buds, head not yet free from yolk sac, fused mouth). In precocial species, hatching occurs later, and the individual leaves the egg (or is born viviparously) as a juvenile. Although these two evolutionary processes can operate independently, altricial species typically have an indirect and protracted development, whereas precocial species exhibit a compressed, direct developmental timetable.

Most definitions of the larval period begin with hatching. However, the phrase "larval period" is applied very loosely and varies from beginning at either hatching or the onset of exogenous feeding (reviewed in Urho 2002). Although commonly used as an ontogenetic reference point, the relevance of hatching as a key developmental event is in dispute (Balon 2001). Nonetheless, hatching is a significant time point with respect to the animal's visual ecology and defines a transition between two different types of selective pressures on visual development (Urho 2002). Prior to hatching, developmental constraints prevail, whereas after hatching, ecological constraints become more important (Figure 1). Altricial species hatch with a relatively simple retina and do not complete retinal development until late in larval life (Figures 2 and 3). As retinal development continues, they are subject to the ecological pressures of foraging and predation. In contrast, precocial species complete retinal development before hatching, when developmental constraints predominate. In both cases, the larval form is a life history period during which organ systems are undeveloped relative to the adult (Hall and Wake 1999). During this period, organisms invest in growth (i.e., in size), and the organ systems develop later. In many species, the larval form is retained over a protracted period, and it is

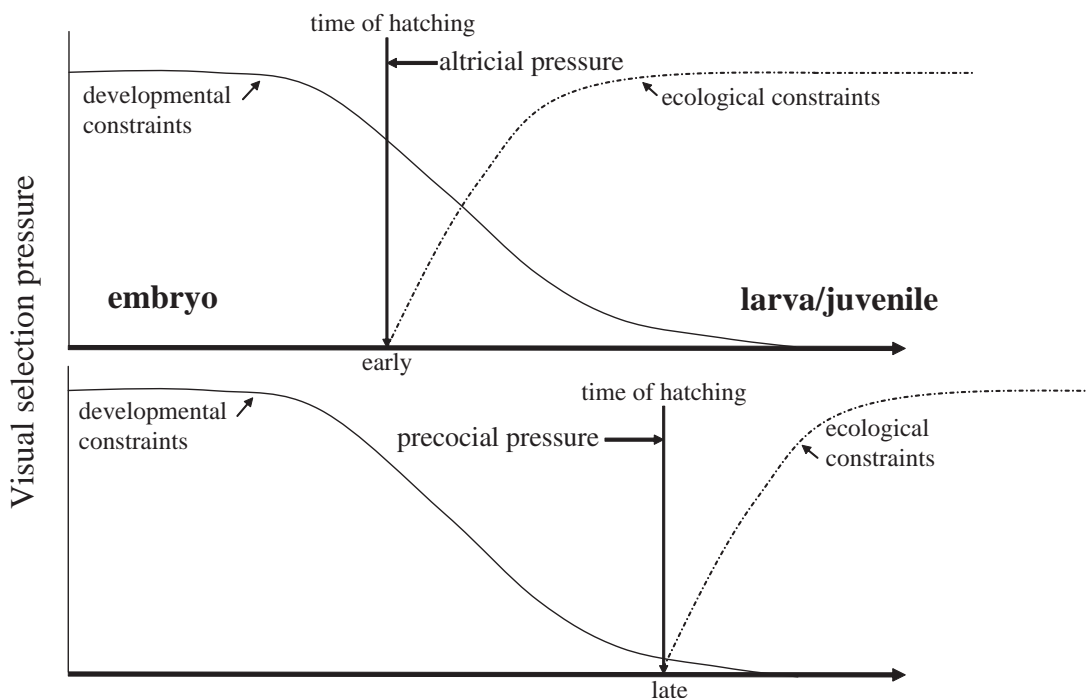


Figure 1. Schematic diagram illustrating how hatching can be seen as representing a transition between periods of the life history affected by developmental versus ecological constraints. Upper panel: Altricial species reduce parental investment in the egg and hatching occurs at an earlier developmental stage. Visual development continues after hatching and is subject to ecological-environmental pressures such as foraging and predation. Lower panel: Precocial species increase parental investment in the egg and hatching occurs at a later developmental stage. At hatching, visual development is nearly complete and ecological constraints predominate.

useful to evaluate whether retinal characters expressed by these larvae are merely immature traits or are specific adaptations to the larval lifestyle (see below).

Fish larvae must feed to grow. Thus, the first features to appear in the retina should maximize foraging success. In general, at the onset of exogenous feeding, fish larvae exhibit limited visual acuity and are indiscriminate in their choice of food items (e.g., Dill 1977; Houde and Schekter 1980; Batty 1984; Brown and Colgan 1985; Munk and Kiorboe 1985; Blaxter 1986; Browman and Marcotte 1986, 1987a, 1987b; Colgan et al. 1986; Drost 1987). Growth rate is a major indicator of survival in red drum *Sciaenops ocellatus* larvae (Fuiman and Cowan 2003), and in most fish, acquisition of more efficient foraging behavior is generally rapid (Blaxter 1968, 1986; Balon 1986). During the early larval period, the probability of marine larvae escaping predator strikes is low (Folkvord and Hunter 1986). Early

stages of larval Atlantic herring *Clupea harengus* rely on transparency to avoid detection and use mechanoreceptive cues to reduce the probability of capture (Blaxter and Fuiman 1990; Fuiman 1993). Older, more opaque larvae begin to use visual cues to actively evade capture (Fuiman 1993). We suggest that visual capabilities mediating vigilance for predators are not cost effective during the early stages of altricial larvae, but become increasingly important as the larva grows.

Ecophysiology and Ecomorphology of the Fish Retina

Most adult fishes have a well-developed eye, effective for prey location and predator detection (Browman et al. 1990; Hawryshyn 1997). The structure of the fish eye is typical of that for all vertebrates, where incident light is focused by the cornea and lens onto the photoreceptor cells. Unlike the organization of the invertebrate retina,

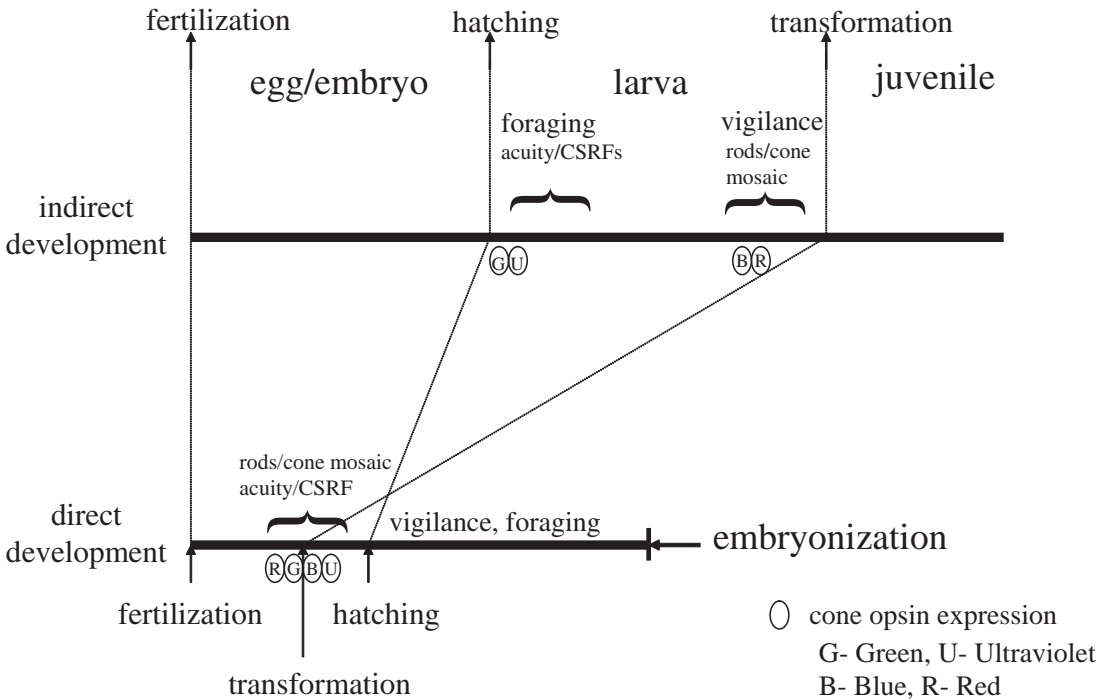


Figure 2. Schematic diagram illustrating how embryonization compresses the fish's early life history, such that, eventually, all retinal development is completed prior to hatching. Altricial species complete development in the face of ecological constraints. Initially, the dominant constraint is foraging and larvae maximize acuity for successful prey location. At later stages, the appearance of rods and the cone mosaic provide low light and motion sensitivity that underlie vigilance for predators. Precocial species hatch as juveniles, with the retina fully equipped for both foraging and vigilance. The sequence of cone opsin expression is not conserved between indirect and direct development.

photoreceptor cells of the vertebrate retina point backwards, away from the incident vector of light (Figure 3). Photons must pass through the entire neural retina before being captured and transduced into neural impulses by the photopigments contained in the outer segments of the rod and cone photoreceptor cells (Schnapf and Baylor 1987). Light information then travels back through the retina as neural impulses and is processed by horizontal, bipolar, and amacrine cells before being relayed to the ganglion cells (Dowling 1987). Visual information from the retina travels to the brain along the optic nerve as action potentials running through the ganglion cell axons (Wulliman 1997; Kandel et al. 2000). The details and discriminability of the visual image (predator or prey) that reaches the brain via these axons will depend on the signal processing capability of the retina.

To be effective, the photoreceptors must be sensitive to at least some of the wavelengths and

intensities of ambient light, and the retina must have sufficient acuity to resolve ecologically relevant objects. Sensitivity is the range of intensities and wavelengths that the retina can transduce. Acuity refers to the spatial resolution of the retina. The aquatic environment exhibits high variability in the intensity and spectrum of ambient light, and fish, as a group, display many adaptations associated with this, both ontogenetically (Beaudet and Hawryshyn 1999; Bozzano and Catalan 2002; Kroger et al. 2003) and interspecifically (Myrberg and Fuiman 2002; Evans, in press).

Photoreceptor Structure and Function

A typical fish retina contains both rod and cone photoreceptor cells, distributed throughout the retina (Fernald 1988). Rods dominate the retinae of deep-sea and nocturnal fishes (Wagner et al. 1998), as well as fishes in deep, freshwater habitats (Cowing et al. 2002a). Cones dominate in

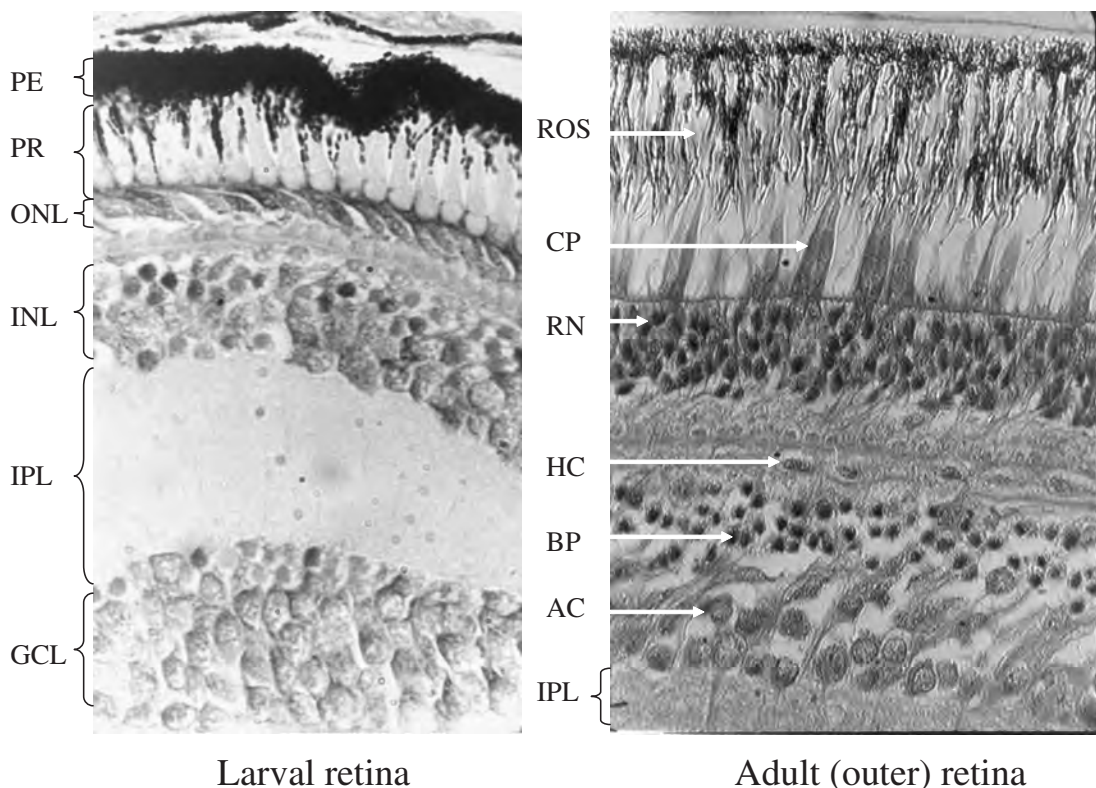


Figure 3. Photomicrograph illustrating the lamination present in the larval retina (left) of winter flounder *Pseudopleuronectes americanus*. The adult retina (right) exhibits similar lamination, but the complexity of each layer is much greater than that of the larva. The retinae are cross-sectioned and oriented with the sclera to the top. PE: pigmented epithelium; ONL: Outer nuclear layer; INL: Inner nuclear layer; IPL: Inner plexiform layer; GCL: Ganglion cell layer; ROS: Rod outer segment; RN: Rod Nuclei; PR: Photoreceptor; CP: Cone photoreceptor; HC: Horizontal cell; BP: Bipolar cell; AC: Amacrine cell.

fish that inhabit photopic (bright light) environments (Collin and Collin 1988), although rods are also present for vision under scotopic (twilight) conditions. The spatial distribution of photoreceptors in the retina varies as a function of ambient light quality. In some fishes, rods dominate in the dorsal retina (Kunz et al. 1985; Nag and Bhattacharjee 1989); in others, they dominate in the ventral retina (Evans and Fernald 1993). There are also distinct regional distributions of cone spectral classes (e.g., Levine and MacNichol 1979), with specific adaptations being related to variations in the intensity, wavelength, and directionality of environmental light (e.g., Munz and McFarland 1977) and the behavioral ecology of the fish (Lythgoe 1984).

Rods and cones differ in threshold sensitivity to quanta of light energy; rods are at least one

order of magnitude more sensitive than cones (Baylor et al. 1979). Scotopic vision is rod-mediated, and individual receptor cells can respond to a single photon absorbed by a photopigment molecule in the outer segment (Baylor et al. 1979). Rods may also be sensitive to minute changes in light intensity (Hamer 2000). Photopic vision is cone-mediated, and these receptors are much less sensitive. In the torrentfish *Cheimarrichthys fosteri*, the scotopic threshold is $5.328 \times 10^{-8} \mu\text{Einstein s}^{-1} \text{m}^{-2}$ whereas the photopic threshold is $1.866 \times 10^{-2} \mu\text{Einstein s}^{-1} \text{m}^{-2}$, a difference of six orders of magnitude (Meyer-Rochow and Coddington 2003).

Historically, rods and cones were classified solely by their outer segment morphology (Walls 1942). Rod outer segments are typically long, slender structures, while cone outer segments are

shorter and tapered. The morphology of many cones, and the absolute sensitivity of some cones (e.g., to ultraviolet [UV]), is rod-like (Hawryshyn 1991). In these fishes, the ultrastructural organization of the outer segment membrane has been examined to clarify the classification of photoreceptors as rods or cones (Pankhurst 1984). More recently, rods and cones have been distinguished by using antibodies against specific rod or cone opsin proteins (Molday and MacKenzie 1983) or by using riboprobes to opsin mRNA (Raymond 1993; Helvik et al. 2001; Forsell et al. 2002).

Transduction of Light Information

Phototransduction occurs in the outer segment of the photoreceptor. The densely stacked outer segment membranes contain photopigment molecules that absorb photons of light (Applebury and Hargrave 1986). These visual pigments consist of opsin, a membrane protein comprised of approximately 350 amino acids (Nathans and Hogness 1984), plus a chromophore bound to the opsin (Kropf 1972). Rod and cone photoreceptors use vitamin A₁ and/or A₂ based chromophores. The chromophore absorbs light energy; the opsin protein modifies the spectral absorbance of the chromophore. The spectral absorbance of fish visual pigments can range from the far-red (Levine and MacNichol 1979) to the ultraviolet (Harosi and Hashimoto 1983; Hawryshyn 1997; Collin and Marshall 2003). This can occur as a result of either changes between vitamin A₁ and A₂ ratios in the chromophore (Beatty 1975) or changes in the amino acid sequence of the opsin protein (Archer et al. 1995; Hope et al. 1997; Carleton and Kocher 2001; Cowing et al. 2002a, 2002b). For example, single amino acid substitutions can change the peak absorbance of the opsin from 2 to 35 nm via alteration in the three-dimensional structure of the protein, which changes the probability of photon capture at a given wavelength (Archer and Hirano 1996; Hunt et al. 1996; Carleton and Kocher 2001).

Although the majority of photoreceptors express one photopigment, the outer segment membranes of some cells contain pigment mixtures (Parry and Bowmaker 2002). This can be a result of using both vitamin A₁ and A₂ chromophores with one opsin (Beatty 1975; Loew and Dartnall 1976; Bowmaker et al. 1988) or two distinct opsins with the same chromophore (Shand et al.

1988). These processes may serve to extend the habitat range of some fishes, allow them to migrate between light environments with relative ease (e.g., Shand et al. 2002), or acclimatize them to seasonal changes in light spectral properties (Loew and Dartnall 1976).

Wavelength Discrimination

Color vision—the ability to discriminate between different wavelengths of light—requires multiple photoreceptor types differing in peak wavelength sensitivity (Marks 1965; Stell and Harosi 1976; Dowling 1987). Wavelength discrimination improves visual contrast between objects and the background (Munz and McFarland 1977), and fish from photopic habitats have multiple cone phenotypes differing in their wavelengths of maximum sensitivity (Lythgoe 1972, 1984). The adult teleost retina usually has three to five different cone opsins, but only one type of rod opsin (Levine and MacNichol, 1979). Rod-mediated wavelength discrimination is rare and only possible when multiple rod types are present. Although multiple rod phenotypes are present in frogs (Nir and Papermaster 1983), this has not been reported for teleosts.

The Cone Mosaic

An intriguing morphological feature of the fish retina is the cone mosaic, a regular geometric pattern of cells in the various retinal layers (e.g., Engström and Ahlbert 1963). There are many variations of the cone mosaic, and the pattern can vary spatially within one retina, as well as ontogenetically. One of the most common patterns is the square cone mosaic (Collin and Shand 2003; Figure 4). The spatial arrangement of the inner retinal layers is coordinated with that of the cone mosaic (Wagner 1975; Cook 2003), and the photoreceptor spacing is reflected in the inner retinal circuitry. For example, bipolar cells show a regular lattice structure that parallels that of the cone mosaic (Podugolnikova 1985), and the geometry of horizontal cell placement coincides with that of the cone mosaic as it is formed (Hagedorn and Fernald 1992; Hagedorn et al. 1998; Collin and Shand 2003). Fish relying on photopic vision typically have well-ordered mosaics, especially when their prey are fast moving (Lyll 1957). The mosaic becomes less organized in fish from habitats

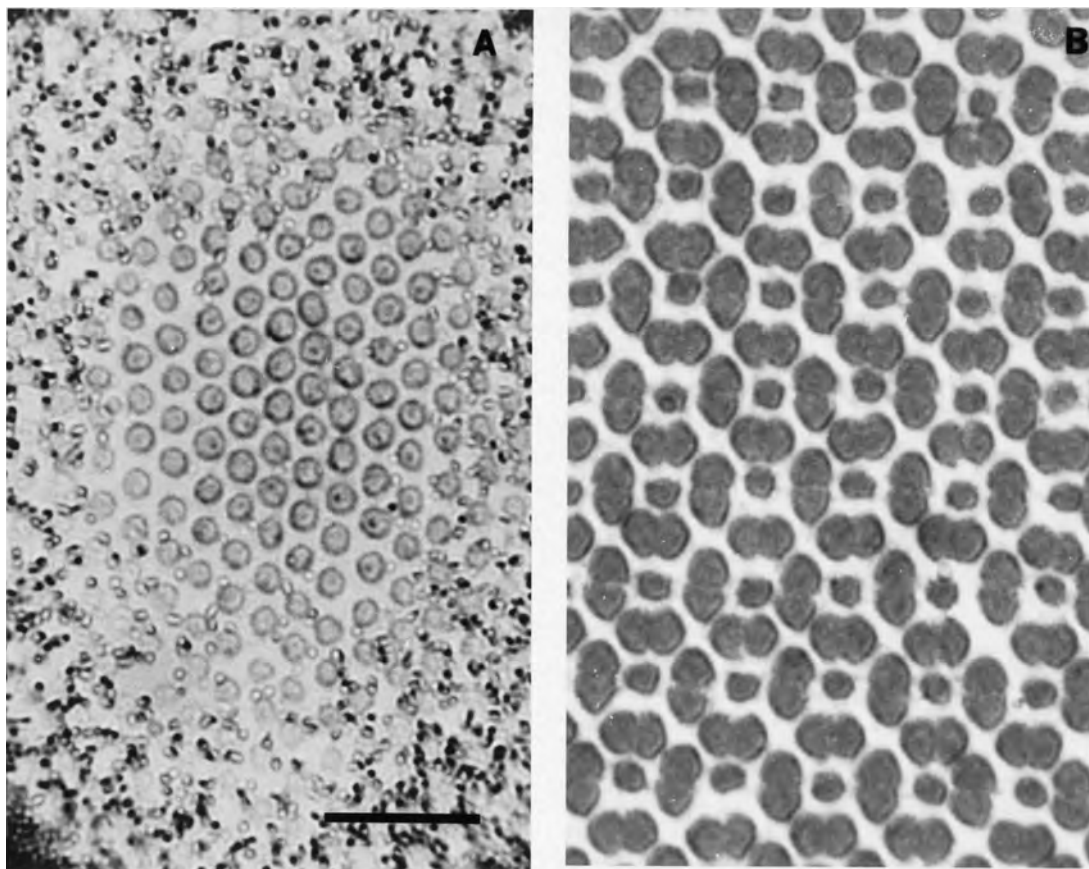


Figure 4. Photomicrograph of tangential sections of winter flounder central retina illustrating the arrangement of cones in larval and adult stages. Left panel: larva 1 day posthatch (dph), with a hexagonal array of single photoreceptors. Right panel: 2-year-old fish (10 cm TL), exhibiting the square cone mosaic of four paired cones surrounding a central single cone. Scale bar 10 μ m.

with reduced ambient light intensity (Meyer-Rochow and Klyne 1982; Land 2003). Nocturnal and deep-sea fish do not have a cone mosaic (Engström 1963; Braekevelt 1984, 1994; Sandy and Blaxter 1980). The presence and type of cone mosaic is taken as evidence of good visual capability in fish, but despite such mosaics having been a significant focus of research, just how they contribute to visual capabilities is not known (Cook and Chalupa 2000; Cook 2003).

Retinal Circuits in Wavelength Discrimination, Target Detection, and Target Contrast Enhancement

The ability to detect predators and prey depends upon the retina's sensitivity to light, its spatial

acuity, and its ability to discriminate wavelengths. Acuity is partly determined by the spatial density of photoreceptor cells in the retina (e.g., Browman et al. 1990). To increase visual acuity, cones are often closely spaced, and there is one ganglion cell for every cone (although this is highly variable). High densities of cones are typically observed in retinal areas involved with prey location (Collin 1988; Browman et al. 1990; Shand et al. 2000). Even some deep-sea fish with rod-dominated retinæ have an area of single cones in the region of binocular vision (Lockett 1977; Munk 1981, 1982, 1989). To increase visual sensitivity, rods are also closely spaced, and many rods converge onto one ganglion cell. In deep-sea fish, these rods are often packed in bundles forming macroreceptors of varying cell numbers (Land

2003) or banded in several layers (Warrant et al. 2003).

Although necessary, good acuity and sensitivity are not sufficient to allow image formation. In the vertebrate retina, the basis of higher order image formation is the center-surround receptive field (CSRF). Information from the photoreceptors is not sent directly to the brain, but the retina first extracts features of the image, such as contrast (Kandel et al. 2000). Such brain-like processing is not surprising given that the neural retina of vertebrates is a component of the central nervous system and its laminar structure is similar to that of the brain (Dowling 1987). In fish, CSRFs further increase visual acuity and enhance contrast sensitivity (Burkhardt 1977; Bilotta et al. 1995; Hawryshyn 1997). Photoreceptor cells form the receptive field of a ganglion cell. These photoreceptors can excite or inhibit horizontal cells, allowing for lateral control of the neural signal to the bipolar and ganglion cells. As a result, ganglion cells may be excited or inhibited by light in the center of their receptive fields, depending on whether they receive input from "on" or "off" center-surround fields (Hawryshyn 1997). In adult fish, CSRFs also integrate input from cone photoreceptors of different wavelength sensitivity (Burkhardt 1977; DeMarco and Powers 1991; Bilotta et al. 1995). Thus, CSRFs are also important for the perception of complementary colors (blue/yellow, red/green) and in color constancy (the ability to subtract background color across a range of intensities).

The Larval Fish Retina

The retina of the fish larva lacks many of the adult visual capabilities. Histological and molecular examinations reveal that no rods are present in the early retinae of many fishes (Ali 1959; Blaxter 1969; Ahlbert 1969, 1973; Blaxter and Staines 1970; Johns 1977; Boehlert 1979; Branchek and Bremiller 1984; Pankhurst 1984; Raymond 1985; Raymond and Rivlin 1987; Evans and Fernald 1990, 1993; Kvenseth et al. 1996; Higgs and Fuiman 1998; Shand et al. 1999; Helvik et al. 2001). The lack of rods makes the larvae less capable of feeding under low light conditions (Blaxter and Staines 1970). In contrast to the multiple cone phenotypes observed in the adult, the retina of most fish larvae is dominated by

green-sensitive single cones, although cones sensitive to ultraviolet light are also often present (Evans et al. 1993; Britt et al. 2001; Helvik et al. 2001). Predominance of one type of cone opsin limits wavelength discrimination-based tasks and reduces target contrast sensitivity.

The retina of the early larval stage has little regional specialization and relatively low acuity. For example, the cone spacing in the retinae of winter flounder allows maximal visual angles of 1.18 degrees per cone. The pure cone retina has a 1:1 ratio of photoreceptors to ganglion cells; thus, the sensitivity is reduced when compared with the adult retina, which has a rod to ganglion cell convergence ratio of 7.5 to 1 (Evans and Fernald 1993). Retinae of altricial fish larvae are composed predominantly of one cone phenotype that is maximally sensitive to green light (Evans et al. 1993; Britt et al. 2001; Helvik et al. 2001). Therefore, even if CSRFs are present in larval retinae, color contrast is impossible (Kamermand et al. 1998). The presence of CSRFs in fish larvae, their contribution to the development of visual acuity, and their importance to the visual capability of larval fishes all remain to be determined.

In addition to late appearance of rods, the cone mosaic also arises late in the retinal ontogeny of many teleost species (Cook 2003; Evans, in press). Cone mosaics are thought to enhance predator avoidance. For example, Ahlbert (1973) noted an increase in motion sensitivity in Eurasian perch *Perca fluviatilis* at the time of cone mosaic appearance. The developmental time point when the mosaic first appears could be a significant indicator of the ability of larvae to respond visually to predator attacks.

Rods, cone mosaic, and higher order visual processing each make significant contributions to the visual ecology of adult fish. Their absence from the larval retina suggests inferior vision. However, the visual system need only meet the larva's needs in finding prey and in perceiving danger. If fish larvae are subject to selective pressure for better vision, there should be a correlation between the timing and variation in retinal development and the demands of foraging and predator evasion. This assumes, however, that good vision alone will increase foraging success and predator evasion, but other factors such as swimming ability and other sensory modalities will also play a role.

Development of Vision and Visually Mediated Behavior

The retina mediates numerous visual functions. Knowledge of the relationship between retinal structure and behavioral capability should allow us to infer those environmental pressures most important at each stage of development. Foraging success, especially for small particulate prey, is dependent upon visual acuity and contrast sensitivity (Blaxter 1991). Despite the variation in timing of retinal development, many species seem to have a similar degree of spatial resolution when they begin exogenous feeding (5–7 degrees) (Carvalho et al. 2002). Retinal acuity is determined by cone spacing, cone to ganglion cell convergence, and CSRF organization. Visual target contrast is augmented by the presence of multiple cone phenotypes and CSRFs. Predator vigilance is likely augmented by sensitivity to motion and low light intensity (Blaxter 1986). Sensitivity is a function of the rod cell absolute sensitivity, rod density, and rod to ganglion cell convergence. Motion sensitivity is thought to be mediated by the cone mosaic (Lyll 1957). Each of these features is poorly developed in early larvae, but as retinal development proceeds, increases in visual capability are observed (e.g., Blaxter 1975, 1986, 1991; Carvalho et al. 2002).

Acuity

The acuity of several species of adult fish has been measured and, in general, approaches (within a factor of two) the theoretical maximum expected on the basis of optics and the density of photoreceptors (e.g., Tamura 1957; Tamura and Wisby 1963; Northmore and Dvorak 1979; Hairston et al. 1982; Li et al. 1985). A behavioral index of acuity can also be obtained using the optomotor (OMR) and optokinetic responses (OKR) (Baier 2000). A fish that swims in the direction of perceived motion demonstrates OMR. Eye movements in the direction of perceived motion are defined as OKRs. It is interesting to note that removal of the optic tectum leaves these responses intact (Roeser and Baier 2003), implying that the visual processing underlying the OMR and OKR occurs in the retina.

During the first few weeks of ocular development in fish, new cells are rapidly added to the retina and new photoreceptor types appear (e.g.,

Lyll 1957; Ahlbert 1969, 1973; Blaxter 1975; Otten 1981; Grun 1982; Branchek and Bremiller 1984; Fernald 1984, 1985). Throughout early ontogeny, vision is perhaps the primary sensory modality involved in prey captures (see Iwai 1980; O'Connell 1981; Blaxter et al. 1983; Kawamura and Ishida 1985; Blaxter 1986). Several studies have documented rapid changes in visually guided behaviors of young fish. Optokinetic responses could first be observed in gobiids at a stage when the retina was anatomically poorly differentiated (Fishman 1977). A rapid (within 7 d) increase in visual acuity was observed in herring and plaice, indicating that the photoreceptor complement of the retina was changing rapidly (Blaxter 1975). Otten (1981), working with cichlid fishes, described temporal changes in visual acuity calculated from photoreceptor cell densities. Clark (1981) followed retinal development in larval zebrafish *Brachydanio rerio* (also known as *Danio rerio*) and compared it to the optomotor response. Neave (1984) conducted a similar study on larval plaice *Pleuronectes platessa* and turbot *Scophthalmus maximus*. All of these studies report a rapid increase in visual acuity during the first few days or weeks following hatching. This was manifested at both the behavioral and anatomical levels. Thus, many species show a rapid increase in visual acuity, which is related to successful location of small prey targets (Browman et al. 1990).

Center-Surround Receptive Fields

Both on- and off-CSRFs are present in the adult fish retina, and these CSRFs are wavelength specific (Burkhardt 1977; Beaudet et al. 1993). Lateral inhibition of photoreceptors by horizontal cells forms the center-surround responses of cones, bipolar cells, and certain ganglion cells (reviewed in Yang et al. 1988). Connections between ganglion cells and the on and off bipolar cells occur in the inner plexiform layer (IPL) (Figure 3). Early in development of the cat retina, no stratification of ganglion cell dendrites is present, and CSRFs have not yet developed (Bisti et al. 1998). As the cat retina develops, glutamate pathway activity leads to stratification of ganglion cell dendrites in these lamina, segregating the on and off retinal pathways (Bisti et al. 1998). Stratification is also present in the IPL of the adult teleost retina (Cook and Sharma 1995; Cook 2003), but when these

organizations arise during development of the fish retina is not known.

During development, many fish begin to exhibit a behavioral acuity (OMR and OKR) greater than that predicted by the retinal receptor spacing (Fishman 1977; Rahmann et al. 1979; Neave 1984). It is possible that this increase in functional acuity corresponds to the appearance of CSRFs. Retinal CSRFs project to the optic tectum and their neural networks create a coordinate map of the visual field (Hawryshyn 1997). Rahmann et al. (1979) and Zeutzius and Rahmann (1980) reported that the period of rapid increase in visual acuity was also manifested in the optic tectum by an intensive period of synapse development. We assume that early retinal development mediates foraging success because of an increase in cell density and resulting increase in behavioral acuity. Following from that, we predict that CSRFs should arise early in the development of altricial species to increase behavioral acuity and foraging success.

Rod Development

Cones dominate the early retina of almost all vertebrates. Although rod opsin is expressed before cone opsin in higher vertebrates and some precocial fish (Raymond 1993), the vertebrate cone photoreceptors begin to differentiate well before rods (Mann 1964; Hollenberg and Spira 1973; Branchek and Bremiller 1984). Cones are believed to be ancestral to rods (Okano et al. 1992), and in altricial fish, cones develop first and express cone opsin well in advance of rods (Helvik et al. 2001). Rods are added late in vertebrate neural development and, in fish, continue to be added throughout life (Johns and Fernald 1981; Johns 1982; Raymond 1985; Fröhlich et al. 1995). This sequence appears to hold even for teleost species with an all rod retina in the adult stage (Wagner et al. 1998). The elopomorph fishes appear to be the one exception, as evidenced by the leptocephalus with a pure-rod retina (Braekevelt 1984; Pankhurst 1984).

Retinomotor movements (the displacement of photoreceptor cell types relative to other cells within the retina, in response to a change in light intensity) begin at the same stage that rods first appear (Blaxter and Jones 1967; Blaxter and Staines 1970; Ali 1975; Kunz and Ennis 1983; Neave 1984), and this has been assumed to indi-

cate the onset of rod function. Salmonids change their phototactic responses by swimming up towards light at the time of rod appearance (Ali 1959). Branchek (1984) measured flicker-fusion frequencies of zebrafish larvae from electroretinograms and found a biphasic response as early as 11 d posthatch, an indication of functional divergence of rods and cones. Carvalho et al. (2002) also measured flicker fusion in the Japanese medaka *Oryzias latipes*. An improvement in acuity from 5 degrees at hatching to 1–2 degrees in the adult could also be attributable to rod function. Increases in acuity are observed with increases in rod density (Pankhurst et al. 1993; Fuiman and Delbos 1998). Motion sensitivity also increases with rod recruitment, as fish cannot school or track an optomotor drum (follow a rotating stripe pattern) before rods appear (Blaxter 1986). Startle response of Atlantic herring is also correlated with rod development (Fuiman 1993).

When attributing function to structure, an attempt should be made to ensure that these increases in visual acuity are mediated solely by rods and not by changes in cone abundance or by other changes in neuronal wiring (CSRFs) that increase visual acuity. Given the high degree of variation in retinal developmental timing between species, we should minimize confusion by studying species in which only one retinal feature arises at a time. Otherwise, we may incorrectly attribute function to structures appearing simultaneously. This is especially true with precocial/direct developing species in which the developmental timetable may be compressed. Altricial/indirect species may provide a clearer correlation between the components of retinal development and the onset of corresponding visually mediated behaviors.

Cones and Cone Mosaics

Double cones do not appear in the fish retina until late in retinal ontogeny (Ahlbert 1969, 1973). At varying times during larval development, single cones are reorganized into the adult mosaic (Evans, in press). The change involves both morphology and spectral sensitivity of the cells in each position of the mosaic (Figure 5). The cone mosaic arises from fusion of single cones into double cones, with the retention of some single cones (Schmidt and Kunz 1989; Shand et al. 1999). It should be emphasized that the wavelength sensitivity of each cone is specific to its

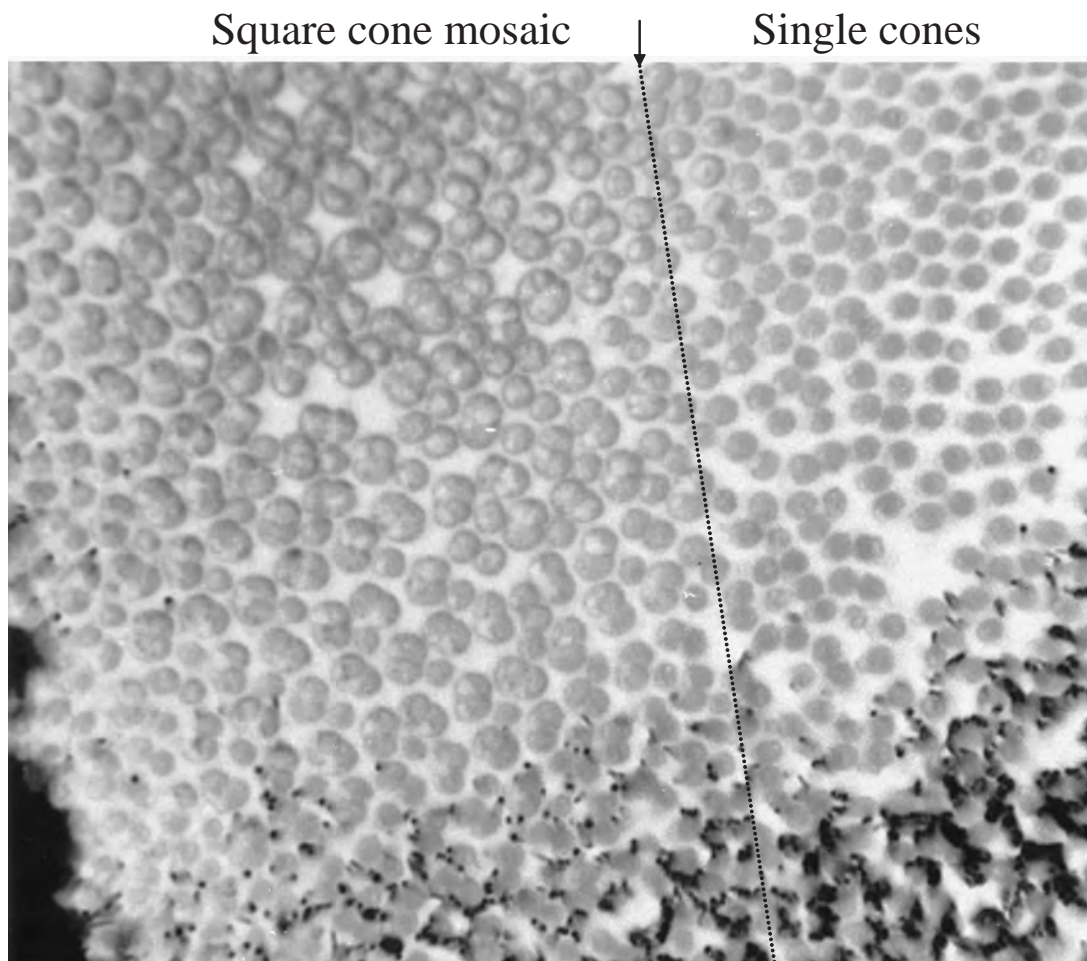


Figure 5. Photomicrograph of tangential section of metamorphosing winter flounder retina, 65 dph. The image illustrates the transformation, which occurs in the functional retina of many fish at the end of the larval stage. The dashed line delineates a region of transition between the single cone phenotype of the larva and the emerging square cone mosaic of the adult.

final position within the mosaic (Levine and MacNichol 1979; Evans et al. 1993; Stenkamp et al. 1996; Stenkamp and Cameron 2002). The central single cone is typically blue sensitive, double cones exhibit combinations of red and green, and corner cones (not shown) are often UV sensitive. During the formation of the cone mosaic, there is regulation between the morphological assembly and the specific wavelength sensitivity of the photoreceptors. Early appearance of the red cones in the goldfish and zebrafish is thought to play a role in the formation of the cone mosaic. The red cones are proposed to be a founder photoreceptor that regulates the other cone photoreceptors dur-

ing formation of the cone mosaic (Wan and Stenkamp 2000; Stenkamp and Cameron 2002). However, we question how the green-cone dominated, larval retina transforms to the adult phenotype in the absence of red founder cones (Evans et al. 1993).

Horizontal and bipolar cells also become arranged in a mosaic pattern (Wagner 1975; Podugolnikova 1985; Hagedorn and Fernald 1992), a functional restructuring of almost the entire retina. One would assume that such a comprehensive structural change must impart a significant advantage to the visual ecology of the animal. The topography of the cone cell mosaic

(square, row, or irregular) also changes during ontogeny (Ahlbert 1969).

Cone mosaics arise before hatching in precocial species, but not until metamorphosis in altricial species. Many other species are intermediate with respect to the timing of cone mosaic appearance (Evans, in press). In some species, flexion and development of fin rays appear to be reliable indicators of when the retina first displays a transition between the larval single cone array and the adult square cone mosaic (Figure 5). Fin and fin ray differentiation leads to an increase in larval swim speed (Fuiman 1993), and escape from predators is more likely when the fish larva can perceive the predator's motion before it initiates an attack (Carvalho et al. 2002). These events may share ecological significance if increased control of swimming behavior, made possible by the fin rays, allows the fish to make better use of a structured retina.

Nonvisual Photoreception

Vertebrate light sensitivity is a function of the lateral eyes, pineal organ, and deep brain. Vision is only possible in the lateral eyes, but even in the retina, rods and cones are not the only light sensitive cells (Bellingham and Foster 2002). The pineal organ consists of differentiated brain photoreceptors and is the main nonvisual photoreceptor of vertebrates. Pineal photoreceptors in teleosts are intracranial with rod-like photoreceptors (Vigh et al. 2002). These are important photoreceptive structures, but have limited neural circuitry and do not mediate image formation (Forsell et al. 2001). Lower vertebrates, such as lamprey and teleost fish, have pineal and parapineal organs that evolved to form the single pineal of higher vertebrates (Meléndez-Ferro et al. 2002; Vigh et al. 2002). In the deep brain, the suprachiasmatic nucleus (SCN) of the hypothalamus is also photosensitive and is the primary pacemaker of the brain (Vigh et al. 2002).

In teleosts, a variety of opsins have been found that do not mediate vision (Drivenes et al. 2003). In particular, vertebrate ancient (VA) opsin and melanopsin are expressed in the retina and brain. Vertebrate ancient opsin was first isolated from teleosts and is a functional photopigment. It is expressed in a subset of horizontal and amacrine cells of the peripheral retina (Philp et al. 2000), but is not expressed in retinal rods and

cones. It is also expressed in the deep brain (Soni and Foster 1997) and pineal organ of fish and is implicated in responses such as circadian entrainment, orientation, and control of body coloration (Drivenes et al. 2003).

Melanopsin is important in the regulation of tetrapod circadian rhythms, and recently, melanopsins have been found in the retina and brain of fish (Drivenes et al. 2003). Like VA opsins, they are not expressed in retinal photoreceptors. In the teleost retina, two types of melanopsin are expressed in amacrine and ganglion cells, but only one type is expressed in horizontal cells. These nonvisual retinal photoreceptors are thought to regulate rod-cone dominance and retinomotor movements (Vigh et al. 2002). Melanopsins are expressed in the horizontal cells of the larval pure cone retina and, thus, may function specifically in cone vision physiology and not just in balancing the responses of rods and cones (Drivenes et al. 2003).

In fish, light sensitivity underlies a variety of nonvisual responses, such as vertical migration, regulation of hatching time, and circadian rhythms. Vertical migration is exhibited in response to changes in light intensity in eyeless Atlantic herring and American plaice *Hippoglossoides platessoides*, demonstrating extra-retinal light sensitivity (Wales 1975). Control of swim depth is attributed to the pineal organ in larval Atlantic halibut *Hippoglossus hippoglossus* (Flamarique 2002). In these larvae, the response to light was observed before the retina began to differentiate, when only the pineal was functional. In Atlantic halibut, the pineal also expresses green and UV opsins (Forsell et al. 2001, 2002).

The pineal organ differentiates and is often functional well in advance of the retina in a number of fish species (Forsell et al. 2001, 2002). Pineal photoreceptors are believed to mediate the observed light-dependent hatching in Atlantic halibut (Forsell et al. 1997). Constant light is found to arrest hatching, and a dark stimulus is necessary for hatching to proceed. The response is thought to be mediated by melatonin, which is synthesized in the dark by the retina and pineal organ (Coon et al. 1998; Falcón et al. 1994). In Atlantic halibut, no retinal photoreceptors were present at hatching; however, the pineal organ was immunoreactive for opsins prior to hatching (Forsell et al. 2001).

Some might argue that the poorly developed

retina of the altricial fish larva is evidence that vision is not important to this stage and that the larval retina is used only for light detection. Non-visual photoreception synchronizes the organism's functional responses to environmental light and is thought to precede vision in evolution. Evidence for this is observed in the acranian lancelet *Branchistoma lanceolatum*, which has no lateral eyes or pineal organ, but possesses brain photoreceptors in a pineal-like region (Vigh et al. 2002). Many mechanisms of light sensitivity exist in fish, suggesting that the eye is present to mediate image analysis. Even in the pure cone state, the retina is a complex structure. When a functional pineal and deep brain receptors are present, there is little need to develop an image forming eye if it is only required as a light detector. The later development of the retina, with specializations for image analysis, supports an important ecological role for the larval eye beyond light sensitivity.

Specializations of the Visual System in Fish Larvae

If vision is key to the survival of fish larvae, we expect to see adaptations related to the visual environment of the free-swimming altricial larva. Does the larval visual system show specializations, and if so, do we see variations in the sequence of ontogenetic events? To assess this, we will concentrate on (1) the timing of rod photoreceptor recruitment to the retina, and (2) the order of appearance of the various cone opsins (phenotypes).

Appearance of Rods

The early appearance of cones, followed by rods, appears to be a general trend throughout the vertebrates (reviewed by Evans and Fernald 1990). In altricial species, rod appearance is delayed until metamorphosis (Figure 2, indirect development). As the developmental timetable is compressed via embryonization, the rods arise closer to hatching time. In precocial species, rods appear early in the embryonic period (Figure 2, direct development). The one exception to this scheme is the leptocephalus larvae of the 700 species of Elopomorpha (eels, tarpon, and bonefish), thought to be the most primitive group of bony fishes (Greenwood et al.

1966; cited in Pfeiler 1986). Found in surface waters at night, they migrate vertically to a depth of 100–600 m during the day. The leptocephalus has a well-developed eye, optic nerve, and optic lobes (Hulet 1978; cited in Pfeiler 1989). The retina, however, is pure rod, confirmed at the ultrastructural level by the presence of membranous disks in the outer segments (Braekevelt 1984; Pankhurst 1984). There is some disagreement as to whether leptocephalus larvae take up nutrients directly from the water or actively feed (Pfeiler 1989, 1999). However, at least one study indicates that they feed on the transparent houses of larvaceans (Mochioka and Iwamizu 1996). In either case, the features described above—which would be selected to increase foraging success—are not as relevant to the leptocephalus as they are to the larvae of other species. Thus, leptocephali may use their pure-rod retina to detect movement of either prey or predators at low light intensity.

Although leptocephali have a pure rod retina, at their first metamorphosis, anguillid eels acquire cones and migrate to freshwater (Pfeiler 1989). When the adults return to the deep ocean, they lose their cones and develop a pure rod retina (Pankhurst 1982). The retinal development of adult eels then follows the same pattern as observed in deep sea fish. In fact, many species of deep-sea fish have a pure cone retina as larvae, but lose the cones at metamorphosis and develop a pure rod retina as adults (Wagner et al. 1998). The similarity in the retinal development of eels and these deep sea fish suggest that the pure-rod leptocephalus retina is a specialization, possibly arising from early activation of the genes controlling rod expression.

Appearance of Multiple Cone Opsins

Although only an extremely small fraction of extant species have been examined, the sequence of cone opsin expression in different teleost species yields some interesting observations. In altricial marine fish species, the larval retina is initially dominated by the single cone phenotype (Blaxter and Staines 1970; Evans and Fernald 1993; Shand et al. 1999). The retinal foveal region of primates is used for high acuity vision and is dominated by single cones expressing one photopigment (Kandel et al. 2000); so, perhaps there are benefits of the single cone retina to the larva. In many

larvae, these cones are green sensitive (Evans et al. 1993; Britt et al. 2001), but with ultraviolet sensitive single cones present in some species (Forsell et al. 2001; Helvik et al. 2001). Although the green opsins predominate early, it is possible that all opsins appear at a similar time in localized regions of the retina (J. V. Helvik, University of Bergen, Norway, personal communication). Timing of opsin expression in the retina can also be location-specific, with different regions showing different timing in the expression of the various opsins. The sequence of appearance of cone opsins in altricial species is green opsin predominating early, with UV also present in localized regions. Red and blue spectral sensitivity appear later (Britt et al. 2001; Evans et al. 1993), but prior to cone mosaic formation (Helvik et al. 2001). Precocial/direct developing species express multiple cone opsins before hatching, and the order of cone opsin expression is different from that of altricial species (Figure 2). For example, in the goldfish and zebrafish, the embryonic sequence of visual pigment expression is red, green, blue, then ultraviolet (Raymond et al. 1995; Stenkamp et al. 1996). Based upon cDNA sequences, the phylogenetic order of cone opsins is believed to be red, violet, blue, and then green. Vertebrate long wave cone opsins are thought to be the oldest, or first to arise phylogenetically, with green cone opsins arising last, followed by rod opsin (Moutsaki et al. 2000).

Variation in the developmental timing of cone opsin expression is likely a heterochronic event (Hart and Wray 1999), a switch in the timing of opsin gene expression, such that the green cone phenotype dominates the marine altricial larval retina. Heterochrony is the change in relative time of appearance of a character during phylogeny (Gould 1977) and is a mechanism for generating altered morphology during evolution (Hall 1984). Such heterochrony is described in the development of *Salvelinus* species in different habitats (Balon 1985). Heterochrony is observed in many organ systems, and many traits differ in timing of appearance as a consequence of environmental needs. Such shifts in developmental timing allow retinal characters, such as rods or expression of certain opsins, to appear early or late in ontogeny.

The purpose served by the predominance of green sensitive cones in altricial larvae is not known, but it may increase visual contrast. The wavelength sensitivity of actively foraging larvae is important to their survival. Altricial spe-

cies are free-swimming and subject to foraging pressure once the yolk is resorbed. Thus, the type of opsin expressed would be under selection pressure to increase foraging success (Figure 1). Precocial species complete much of their development before hatching. Because the embryos are not actively swimming, the order of cone opsin expression may be unimportant as long as the necessary opsins are present by the time the fish hatch. Thus, the timing of the specific cone opsin expression may differ between precocial and altricial species depending upon the predominance of developmental constraints before hatching versus ecological constraints after hatching (Figure 1).

These conjectures require studies using a whole life history approach, where embryonic and larval development are integrated with various aspects of developmental biology and behavioral ecology. The retina does not develop in isolation, but in the context of the whole animal and its environment-ecology (sensu Browman 1989).

Conclusions

The presence of a sensory organ capable of higher order image processing is compelling evidence that vision is an important sensory modality for larval fish. Differences in retinal morphology and ontogenetic sequence may be a result of the changes in selective pressure that occur when the position of hatching time varies within a developmental program. Prior to hatching, developmental constraints take precedence, whereas after hatching, ecological constraints become relevant. The protracted nature of retinal development in fishes with altricial larvae may be a consequence of further separation of the selective pressures of foraging and predator vigilance.

In general, the variation in retinal development observed in larval fish is a product of the reproductive strategy of the parent fish. Altricial species with protracted development hatch with a need to forage, and the pressure on retinal development is to increase acuity. This is mediated by cone photoreceptor cell spacing and presumably the organization of CSRFs. As the fish approach flexion and metamorphosis, they develop cone mosaics and rods, presumably in response to predation pressure. In contrast, precocial species develop the retina early during the embryonic period, but the main sequence of development is retained. At hatching, the retina

is fully functional for both foraging and predator vigilance.

The timing of retinal development varies significantly between altricial and precocial species, but the differences are not solely due to the developmental rate. The presence of a pure rod retina in the leptocephalus larva, and the green sensitive cone retina of altricial marine species, lends support to the view that the larval retina exhibits specializations that may have come about through a variety of evolutionary processes. Development is controlled epigenetically, and evolution acts by altering development. Therefore, epigenetic control plays an important role in evolution (Hall 1983). Visual development is likely a product of evolutionary history, developmental constraints, and foraging and predation pressures. An organism must be a functional unit, and attempts to increase foraging success and/or predator avoidance will only be successful if the entire organism is in synchrony with the changes in the stage (Balon 2001, 2002; Kovac 2002).

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