

Metamorphosis and Fish Vision

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SUMMARY

Many species of fish exhibit metamorphosis in which dramatic external transformations occur as a consequence of coordinated changes in gene expression within an organism. Because postembryonic development and change appears to be the rule rather than the exception in teleost fish species, we view metamorphosis as one of many developmental strategies in fish which have continued plasticity as a common theme. Metamorphic changes are manifested in the visual system by modification of photoreceptor peak sensitivity, rod photoreceptor cell addition, and retinal reorganization. These changes correspond to significant changes in the natural habitat of the animal and in its visual capabilities as demonstrated behaviorally. Thyroxine is the main metamorphic hormone as has also been found in amphibia. The

sequence of metamorphic events occur in all teleosts, but they are compressed in time in direct developing animals suggesting that such animals might prove useful for understanding the evolution of metamorphosis in fish. It seems likely that rod photoreceptors may have evolved in conjunction with the change from larval to juvenile stage through metamorphosis in indirect developing fishes. During evolution, the contraction and/or loss of the larval stage has resulted in earlier appearance of rod photoreceptors during development although they always arise later than cone photoreceptors. This ontogenetic developmental sequence supports Walls's (1942) proposal that cones are phylogenetically older than rods and suggests that rods may have evolved several times.

When Gregor Samsa woke up one morning from unsettling dreams, he found himself changed in his bed into a monstrous beetle.

—Franz Kafka, *The Metamorphosis*, 1915

In his novel, Kafka uses the image of metamorphosis to portray the abrupt character of change, which for Samsa has distinctly negative consequences. Among animals, such change is the prelude to a new life, one with significant advantages, and presumably unburdened by memories of the past. In metamorphosis, dramatic external transformations occur as a consequence of significant coordinated changes in gene expression within an organism. Although it is not commonly known, many species of fish metamorphose during postembryonic life, generally changing from transpar-

ent, surface-dwelling larvae to pigmented, benthic-living adults. This typical habitat change is accompanied by dramatic differences in the visual environment (Youson, 1988). Metamorphic changes are not stimulated by such habitat changes but rather prepare animals for their new life-style and hence precede it.

In this paper, we will review evidence about (1) the relationship of metamorphosis to overall developmental strategies in fish; (2) the changes that occur in the fish visual system at metamorphosis, particularly the renovation of retinal structure; (3) the hormonal control of metamorphic change in fish; (4) the differences in visually dependent behavioral performance between pre- and postmetamorphic fish, and (5) the systematic relationship among fish that metamorphose. We will use the term *metamorphosis* to mean an abrupt transformation of features of the animal not related to reproduction that occur after a prolonged period of growth with little morphological change (Just, Kraus-Just, and Check, 1981).

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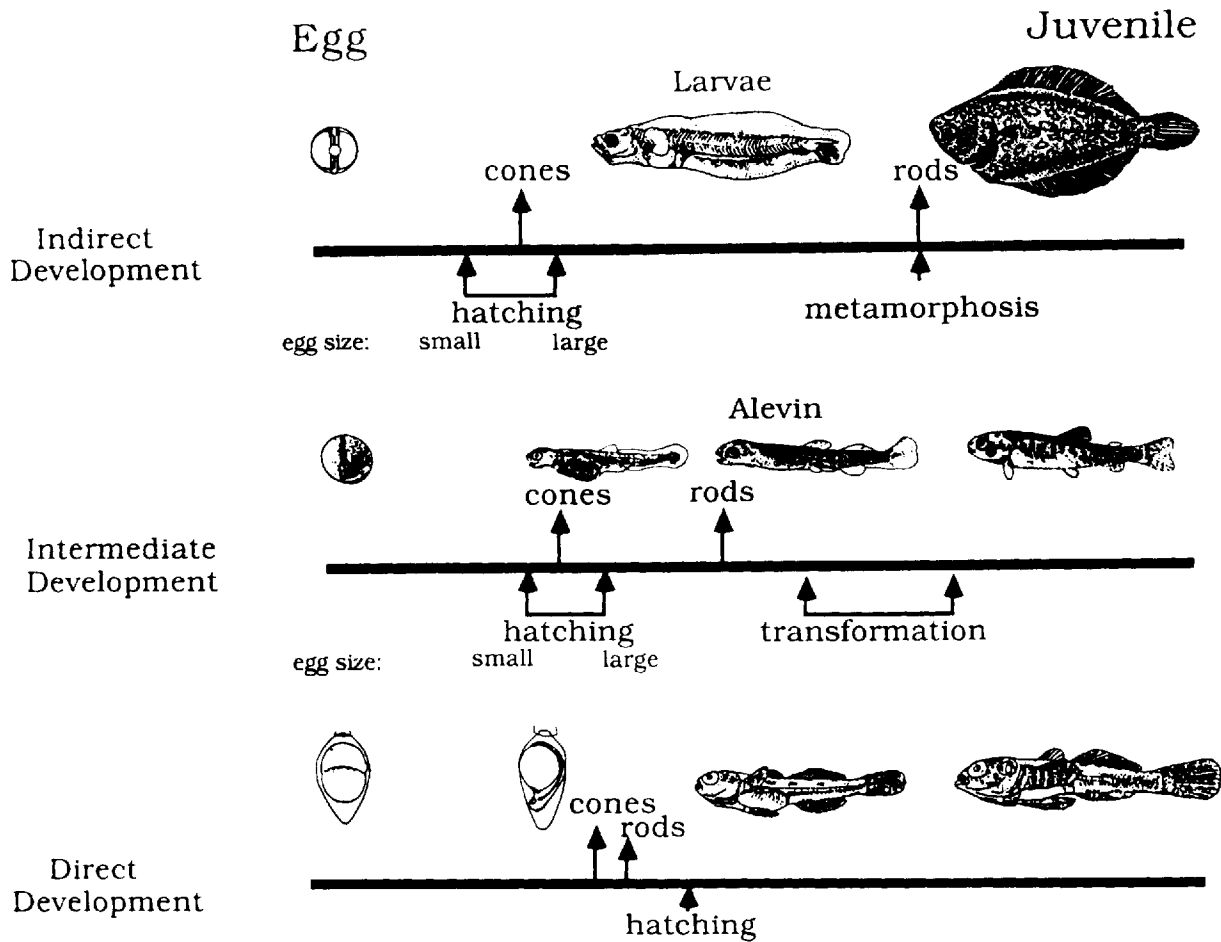


Figure 1 Life history strategy and photoreceptor neurogenesis. Schematic illustration showing the *relative* time of occurrence of developmental events in indirect, intermediate, and direct developing fish species. For salient developmental events, the relative amount of developmental change that has occurred up to that point, not real time is shown. For example, indirect developing species are much less developed at hatching than are direct developing species. The timing of rod and cone appearance during development is indicated by arrows.

Although descriptions of events and presumed mechanisms will be presented, we also suggest some possible selective pressures for specific adaptations. In this way, we hope to identify metamorphic events suitable for future cellular and molecular dissection of fundamental biological processes.

DEVELOPMENT AND METAMORPHOSIS

Despite the great diversity amongst fish species, it is possible to divide teleost developmental programs into the three broad classes: indirect, intermediate, and direct development (Fig. 1). Typically, development proceeds from an egg to a larvae which then transforms into a juvenile (Balon, 1985). Transformations may include changes in

pigment pattern, body shape, fin migration, photophore formation, loss of elongate fin rays and head spine, eye migration, and scale formation (Matsuda, 1987). Such changes may be gradual or abrupt and may also be accompanied by a change from planktonic life-style in the epipelagia to either schooling behavior deeper in the pelagia, or a bottom-dwelling, benthic existence (Fig. 2).

Abrupt transformations considered metamorphic are exhibited by most marine pelagic fish and their development strategy is termed *indirect* (Balon, 1985). Gradual transformation occurs in the intermediate condition illustrated by the salmonids (e.g., Fig. 1), in which the alevin stage is considered to be a vestigial larvae (Balon, 1985). Direct development is found generally in coastal marine and virtually all freshwater fish species.

They lay nonbuoyant, demersal eggs, which are larger or greater in yolk density than are pelagic eggs, and hatch at an advanced state of development without a larval stage (Kendall, Ahlstrom, and Moser, 1984). Egg size or yolk density is correlated with evolutionary change in development: Larger eggs can lead to embryonization in which development is accelerated through evolution until free-swimming larvae are incorporated into intraovular development (Matsuda, 1987). Typically this also results in production of fewer eggs. Many deep-sea, bathypelagic fish species produce a few yolky eggs that hatch into relatively advanced larvae (Marshall, 1953). Parental care is found in many direct developing species, particularly those which are viviparous and retain the eggs in the

ovary until juveniles are extruded (Kendall et al., 1984).

The evolution of vertebrates generally is believed to have proceeded from indirect to direct embryonic development (Fig. 1) (Jagersten, 1972; Freeman, 1982), and teleosts are no exception (Balon, 1984). The selective advantage is that fish with direct or accelerated development, bypass the vulnerable larval stage and become adult-like much earlier (Fuiman, 1985). Because metamorphosis is found in taxonomically diverse groups of fish (see below), it may be a convergent rather than homologous trait. From the taxonomic relations reported in the literature, we propose that metamorphosis is widespread *because* it consists of developmental mechanisms that can be utilized

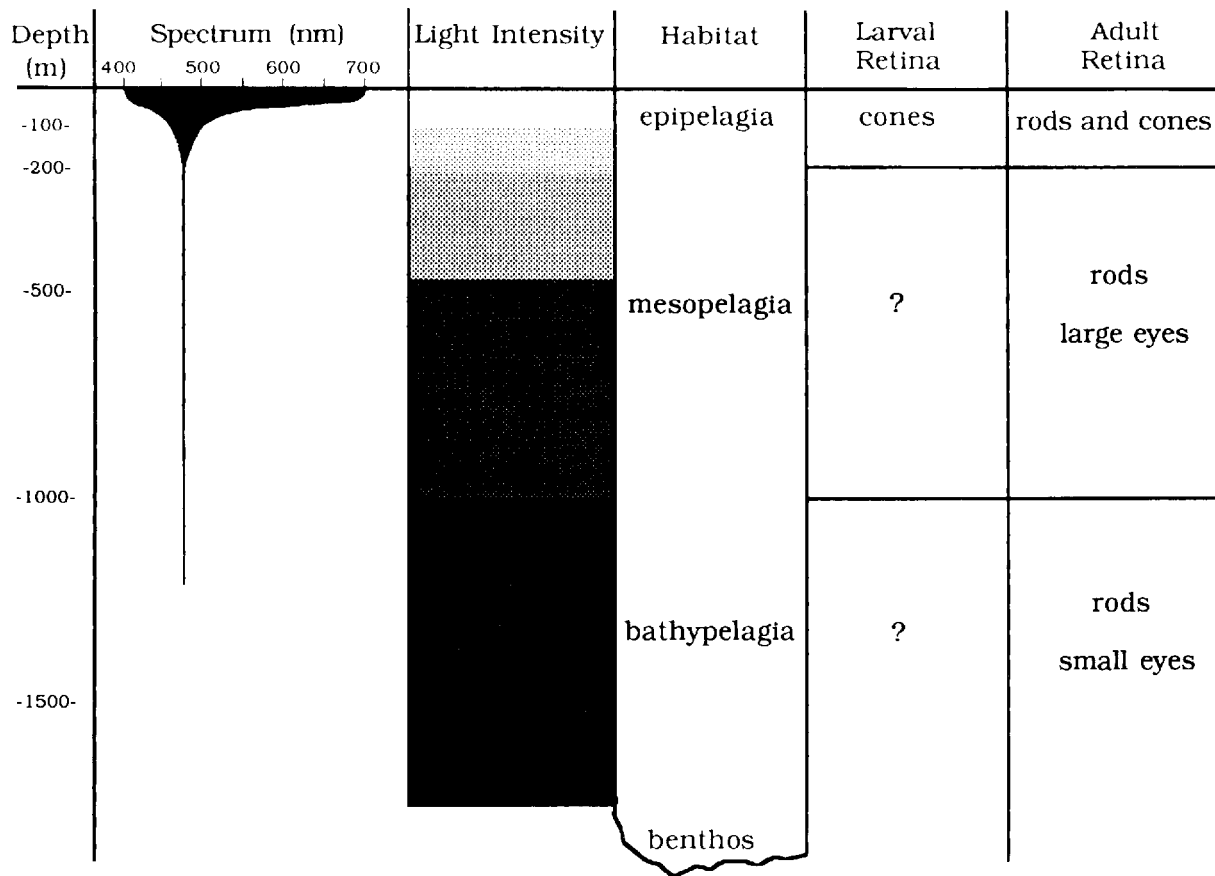


Figure 2 Visual environment and photoreceptor type. The quality of ambient light and corresponding photoreceptor complement are shown schematically as a function of ocean depth. In the epipelagia, light contains all wavelengths, becoming monochromatic with increasing depth, and absolute light intensity decreases exponentially with depth becoming essentially zero beneath 1000 m. In the epipelagia, larvae have pure-cone retinæ and moderate eye size. In the mesopelagia, the adults have large eyes with pure-rod retinæ and retinal structure of mesopelagic larvae are not known. Bathypelagic fish that develop directly or have epipelagic larvae, have small eyes with pure-rod retinæ. Benthic species often have regressed eyes and rely on chemoreception instead of vision.

throughout life. It appears that through heterochronic processes fish have the potential of reactivating developmental programs throughout their lifetimes (Balon, 1983). Alternatively, it is possible that these developmental programs are never entirely deactivated. As a consequence, fish can flourish during environmental changes through morphological remodeling, whether in regeneration of nervous system and body parts or through more profound metamorphic transformations. This capability has undoubtedly contributed to their widespread evolutionary success (Marshall, 1971).

VISUAL SYSTEM CHANGES AT METAMORPHOSIS

As described above, a change in habitat associated with metamorphosis is typically preceded by a change in the animal's physiology. A new visual environment, with the intensity or spectral quality of light altered, requires changes in the biochemistry, physiology, and even anatomy of the visual system (Es-Sounni and Ali, 1985). All elements of the eye, including its location, can be affected by a change in the nature and amount of illumination. When the habitats occupied by larval and adult forms differ dramatically, a gradual change in the organism may not be possible as there is unlikely to be a niche for intermediate morphs.

In virtually all known cases, metamorphosing fish are hatched and live as larvae at or near the water's surface and move deeper under water at metamorphosis. An exception to this pattern occurs in the eels that enter freshwater after metamorphosis. In general, however, the illumination of the postmetamorphic habitat decreases in intensity and becomes effectively monochromatic (Fig. 2). With increasing depth in the ocean, there is a tendency for the eye to become larger, presumably to increase the amount of light captured (Marshall, 1971). Because of the nature of fish eyes, however, increasing eye size results in increased photon capture only when viewing point sources of light (Fernald, 1988, 1990b). There comes a point, however, when the constraints of body size limit any further increase in eye size. One solution has been for deep-sea fish to transform their eyes from a normal morphology to a tubular construction (Fig. 3) (Ali and Anctil, 1976). Such an eye structure, with a large lens, allows greater light capture, a large binocular field, and good depth perception without compromising

the volume occupied by important structures of the head region such as the brain and other sensory systems. At depths greater than 1000 m, there is no longer sufficient incident light to form an image and the eyes of fish tend to again be reduced in size (Marshall, 1971). Detection of bioluminescent organisms may be the only use for eyes of fishes at this depth.

Optics: Cornea and Lens

In amphibia, there are dramatic changes in the lens structure at metamorphosis. In *X. laevis*, the clawed frog, for example, the lens crystallin proteins change in relative concentration (Wistow and Piatigorsky, 1988) and in the toad, *Bufo Marinus*, the lens shape changes as does the corneal contribution to accommodation (Mathis, Schaeffel, and Howland, 1988). The optics of fish eyes however, are different from those of animals living in air in one major respect: underwater there is no air/cornea interface to provide extra dioptric strength. The refractive index of the cornea is nearly identical to that of water, hence, its refractive power is neutralized and all the dioptric strength is concentrated in the lens (Fernald, 1990a). Consequently, for clear vision, the lens is the only optical element of importance so it is perhaps not surprising that there are no reported pre/postmetamorphic differences in the lens structure or focusing power of fish (Table 1 in Fernald, 1988).

Retina

The major sensory surface of the eye, the retina, must be sensitive to important visual stimuli in the environment. Changes in the retina at metamorphosis could occur within individual cell types, by production of new cellular phenotypes, or by changing the interconnection amongst cells. In teleost metamorphosis, all three kinds of change occur, although not in every species. Photoreceptors change their peak sensitivity by altering the visual pigment contained in the outer segments, new kinds of retinal cells are added to the retina, and retinal wiring appears to be rearranged.

Cell Addition. In the vertebrate retina, there are two kinds of receptors, rods and cones. Although many features distinguish them, one fundamental difference is the range of light intensities to which each is sensitive (Rodieck, 1988). Whereas cones are typically responsive to light intensities differing by many orders of magnitude, rods respond over

only a limited range of low-intensity light. In cold-blooded vertebrates, although these differences are still present, they may be smaller (Baylor and Hodgkin, 1974). Retinas typically have a single kind of rod that contains a single species of rhodopsin, maximally sensitive to approximately 510 nm, and several different types of cones with different peak wavelength sensitivities ranging from 400–650 nm. Rods are connected to sum-incident light over a large retinal area resulting in high sensitivity and relatively low acuity. In contrast, cones sample a smaller area, resulting in higher acuity vision.

It has been known for some time that prior to metamorphosis, the larvae of many teleost species have retinas with only cone photoreceptors but they are readily able to feed (see below). Interestingly, the cone threshold for plaice, herring, and sole larvae was lower than expected for a pure-cone retina (Blaxter, 1975). Blaxter and Staines (1970) examined the eyes of 10 families of teleost fish. The eight with metamorphosis had larvae with pure-cone retinas as has been found in the northern anchovy (O'Connell, 1981). Thus, with the exception of eels, it appears to be a general rule that the retina in larval teleosts before metamorphosis has only cone photoreceptors. Rods are added later, sometime after the first feeding as illustrated in the analysis of herring *Clupea harengus* and sole *Solea solea* (Sandy and Blaxter, 1980).

Photopigment Changes. At metamorphosis in many amphibian species, porphyropsin, the vitamin A₂-based photopigment that is considered evolutionarily more primitive (Wald, 1957), is typically replaced by rhodopsin, which is based on vitamin A₁. This has been investigated in the lamprey, in which the visual pigments change during metamorphosis prior to the seaward migrations (Wald, 1957). Pigment differentiation is also observed in metamorphosing eels and salmon before migration (Beatty, 1975; Es-Sounni and Ali, 1985). These visual pigment changes can also be induced prematurely with thyroxine (Wilt, 1959; Cristy, 1974). Based on behavioral observations (see below), it seems likely that comparison of visual pigments in pre- and postmetamorphic teleosts will reveal similar changes in photopigment characteristics.

Retinal Rearrangement. At metamorphosis, an entirely new class of photoreceptors—rods—are added and correspondingly, integrated into the functioning visual system of the animal. Because adult fish have rod-specific bipolar cells, either these cells must be produced, or existing cell types transformed before the rods can become functional. Neither event has been demonstrated. Unfortunately, the only study to compare pre- and postmetamorphic retinal tissue (Sandy and Blaxter, 1980) did not discuss cell addition or modification in nonphotoreceptor layers.

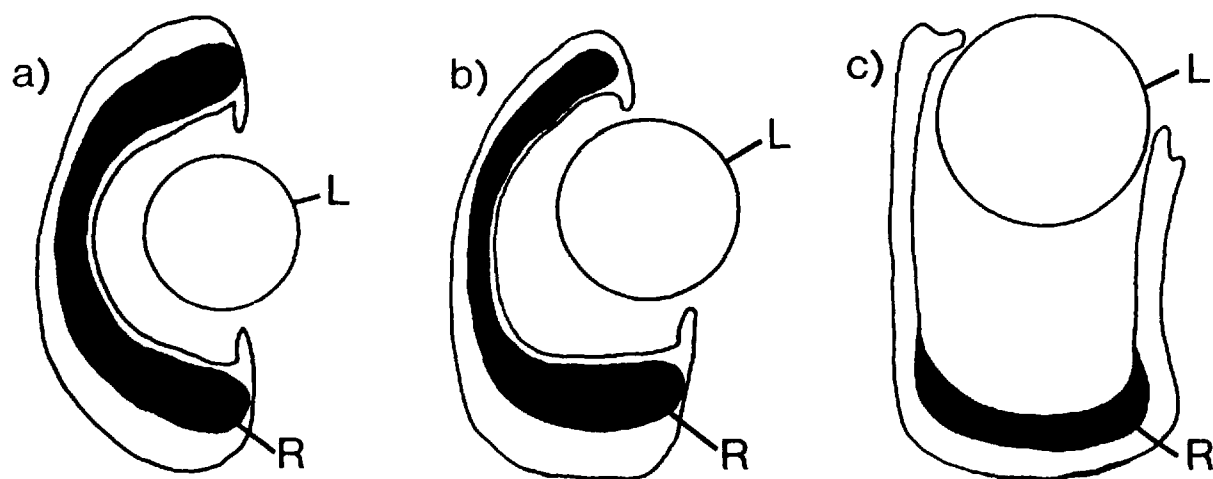


Figure 3 Metamorphosis of tubular eyes. The transformation to a tubular morphology is illustrated for a) premetamorphic; b) metamorphic, and c) postmetamorphic stages. The larval eyes of deep-sea fish have a morphology similar to that of other fishes. During metamorphosis, the eye transforms into an elongate structure to facilitate the increasing lens size without requiring a large eye volume. The tubular eyes have a large lens (L) and the main retina (R) is at the end of the tube. (Figure based on diagrams from Contino, 1939.)

HORMONAL CONTROL OF METAMORPHIC EVENTS

Since the classic experiments of Gudernatsch (1912), it has been clear that hormones play a central role in metamorphosis (Norris, 1983). In addition, environmental cues such as ambient temperature and photoperiod can interact with those internal signals to modulate the timing and duration of metamorphosis.

There is convincing evidence that thyroid hormones play a major role in initiating the first metamorphosis in teleost (bony) fish. Studies on flounder larvae have shown that both triiodothyronine (T_3) and thyroxine (T_4) induce metamorphosis and that antithyroid agents stop metamorphic processes (Inui and Miwa, 1985; Miwa and Inui, 1987a,b). T_3 causes metamorphosis at a concentration several times less than that required for T_4 to have a comparable effect. Consistent with these results, T_4 has been found to increase yolk resorption, growth, development, and survival in several species of fish larvae (Lam, 1980, 1985; Lam, Juario, and Banno, 1985; Lam and Sharma, 1985). In addition, thyroid follicular cells are maximally active during metamorphic climax in flounder and inactive afterwards (Miwa and Inui, 1987a). Cells in the proximal pars distalis of the anterior pituitary, which are immunoreactive to antithyrotropin, are active during metamorphosis. Thus, the pituitary has been implicated in the control of metamorphosis in flounder (Miwa and Inui, 1987a).

Given the important role of prolactin as a regulatory hormone in amphibian metamorphosis, it is puzzling that there have been so few studies of its possible corresponding role in teleosts. Prolactin in teleosts is the freshwater-adapting hormone and also acts as a growth hormone in contrast to its action in mammals (Bern, 1983). It has also been implicated in the differentiation of visual pigments in fish (Cristy, 1974). Wald (1981) speculates that thyroxine and prolactin act in opposition to tightly regulate metamorphosis although this idea has not been tested.

Prior studies of hormone effects on development have measured blood titers of specific hormone levels to infer which factors could cause differentiation. However, the level of circulating hormones is only half the story. Equally important in understanding the role of hormone action is the relative abundance and location of corresponding receptor sites. The number of hormone-specific receptor sites can increase seasonally within spe-

cific brain regions (Habibi, De Leeuw, Nahorniak, Goos, and Peter, 1989) or during the ontogeny of an organism (Carr, Jacobs, and Jaffe, 1981), thereby increasing the animal's physiological sensitivity to a given hormone. Thus, it is clear that some or perhaps many hormones important to development may have been overlooked if absolute blood concentration does not change at the time of critical developmental events. To understand how hormone action precipitates gross morphological changes such as metamorphosis, both hormone titer and receptor density must be measured.

In flounder (Policansky, 1982; Seikai, Tananogon, and Tonaka, 1986) and lamprey (Potter, 1970; Purvis, 1980) metamorphosis occurs sooner when larvae are kept at higher temperatures, although the internal role of hormones is unchanged. This temperature effect has not been analyzed at a cellular or molecular level but it might have a simple biochemical basis.

BEHAVIORAL CHANGES AT METAMORPHOSIS

Metamorphic changes in the visual system could be expected to have important consequences for the behavior of an animal. Because teleosts that metamorphose spend their premetamorphic life with an all-cone retina, the addition of rods should extend the range and variety of visible stimuli.

An important feature of the rod- and cone-containing (duplistic) retinas of lower vertebrates is the relative movement of the photoreceptors and pigmented epithelium as a function of light intensity and time of day (Burnside, Adler, and O'Connor, 1983) (Fig. 4). These retinomotor movements effectively provide the animal with two functionally distinct retinas: All cones during bright, daytime light levels and both rods and cones during dim, nighttime light levels. At high light intensity, the cones contract towards the lens, whereas the rods extend away from the lens and are shielded from incident light by the pigmented epithelial layer (Fig. 4b). At low light levels, this reverses and the rods contract, the cones extend and the pigment granules migrate to the scleral surface of the retina so both photoreceptor types are exposed (Fig. 4c) (Burnside et al., 1983). These retinomotor movements have the important additional feature of increasing significantly the cone-mediated acuity during bright light and rod sensitivity during dim light because each occupies the entire retinal surface at those times (Fernald, 1988). Retino-

motor movements do not occur until both rods and cones are present (Blaxter and Jones, 1967; Ali, 1959, 1975; Blaxter and Staines, 1970) and the

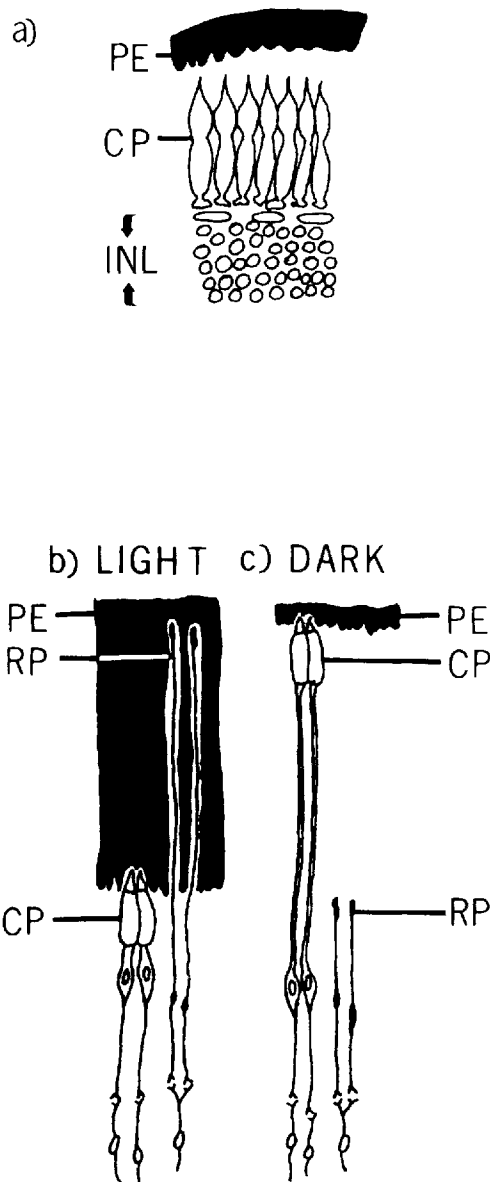


Figure 4 Structure of the retina in pre- and postmetamorphic teleosts. (a) The photoreceptors of the pure-cone retina are illustrated. PE = pigmented epithelium; CP = cone photoreceptors; INL = inner nuclear layer. The PE and CP remain in this configuration under bright and dim light conditions. (b) The postmetamorphic retina contains both rods and cones that undergo retinomotor movements. In bright light, the PE expands to isolate the rod photoreceptors (RP), leaving the cones (CP) exposed to light. In dim light, the PE retracts towards the sclera, the rods retract towards the vitreous and the cones also move sclerad. (Figures b and c are based on a figure from Blaxter, 1975.)

movements are thought to be rod-mediated (Borwein, 1981). Whether cones have the potential for such movement prior to rod neurogenesis has not been investigated. Retinomotor control appears to be local, because illuminating small areas of the retina does not cause retinomotor movements over the whole retina, but only within the area of illumination (Easter and Macy, 1978).

Generally, the pure-cone retina of larval teleosts appears to have light-detection properties intermediate to those of rods and cones and is sufficient to allow the animal to feed and respond to predatory stimuli at moderate light levels (Blaxter, 1975, 1986). Although there have been few reports about how adding rod cells affects specific behavioral acts, several behavioral patterns show dramatic changes during teleost development. Specifically, coincident with rod neurogenesis, phototaxis may reverse signs, an optokinetic response, which depends on visual acuity, is greatly augmented and feeding behavior extends to lower light regimes.

Phototaxis

Phototaxis (movement relative to light) is the simplest visual behavior and it can occur even without an image-forming eye. In early life stages, most teleosts avoid light (negative phototaxis). In Pacific salmon (Ali, 1959) and rainbow trout (Carey and Noakes, 1981), the young are initially negatively phototactic, a response which diminishes throughout development until emergence from the gravel when they become positively phototactic.

The sudden transition in photoresponse of salmonids is coincident with the onset of retinomotor movements which begins when rods become functional (Borwein, 1981), implicating rods in this function. Most marine larvae are found in the bright upper reaches of the water column indicating a positive phototropism, however, Blaxter (1969, 1972) observed that at low light intensity, larval flounder, which possess pure-cone retinæ, were negatively phototactic and only displayed positive phototaxis at high light intensity. The demersal, marine gobiid *Bathygobius soporator* is photopositive at hatching (Tavolga, 1950), possibly because it acquires rods before hatching (Fishman, 1977).

Considering that changes in the sign of phototaxis can occur with the appearance of rod photoreceptors, it is possible that rods aid in migration from one habitat to another or allow switching light regimes during changes in life history stages (Boehlert, 1979). The interaction between rods

and cones allows the determination of absolute light intensity at two levels. The lower light threshold is due to rods. The higher threshold is where the Purkinje shift occurs in dark to light adaptation via retinomotor movements (Blaxter, 1976). Species such as herrings exhibit a daily vertical migration as adults, remaining within a preferred range of light intensity (1–10 mc isolumens; Postuma, 1958 in Blaxter, 1976). The appearance of the rods at metamorphosis would facilitate this behavior.

Optokinetic Response

The most obvious behavior to emerge at metamorphosis is schooling, which depends on optokinetic (optomotor) responses (Shaw, 1970). Prior to the development of the optomotor response, fish are unable to effectively maintain a constant image on the retina and formation of a school is impossible. Schooling is one of the few behavioral patterns that does not occur in herring until metamorphosis (Sandy and Blaxter, 1980). Fish also do not school in the absence of light suggesting that vision is the principal stimulus (Ali, 1959; Glass, Wardle and Mojsiewicz, 1986; Magurran, 1986).

Most species exhibit an optokinetic response that can be used to measure the visual acuity. Typically, as the animal is presented a moving pattern of vertical stripes, the eye(s) fixate(s) on a feature of the visual background and tracks the pattern. As the stripe width is made narrower and/or the speed of movement increases, the animal will at some point no longer be able to follow the movement allowing an estimate of visual acuity (Neave, 1984). In natural situations, such optokinetic responses serve to stabilize an image on the retina either for object or position orientation.

The strength of the optokinetic response improves during development among species utilizing direct through indirect developmental strategies. In a detailed study of the visual ontogeny of the directly developing gobiid, *Bathygobius soporator*, Fishman, (1977) observed a slight optokinetic response when the retina consisted only of cones, with a rapid increase in acuity coincident with the appearance of rods. As the increase could not be attributed to the development of the oculomotor muscles, Fishman (1977) suggested that the onset of retinomotor movements, associated with rod appearance, allowed the embryos to see the stripe pattern more distinctly via light–dark adaptation. Apparently, retinæ must be somewhat

light-adapted for optokinetic responses to occur (Takahashi, Murachi, and Karakawa, 1968).

In species with intermediate development, optokinetic response also indicated an increase in visual acuity with development. In the rainbow trout *Salmo gairdneri* (Rahman, Jeserich, and Zeutzius, 1979), the first optokinetic response occurred in 25% of the animals at 10 days posthatch, but only to a very coarse pattern with 30° of arc. The optokinetic response was observed to rapidly increase to an acuity of 1° arc, in the second half of the larval stage, the stage of salmonid development when rods appear in the retina (Ali, 1959; Carey and Noakes, 1981).

Investigation of optokinetic response of indirectly developing plaice and turbot (Neave, 1984) indicates that acuity estimated from histological measurement (retinal cell spacing) improved slowly from hatching onward, whereas behavioral acuity showed a rapid improvement. Before metamorphosis, behavioral acuity measured 6–7°, whereas histological acuity was 1°–1° 20'. After metamorphosis, the behavioral acuity of 11' surpassed the histological acuity of 40'. Thus, it would appear that some form of transformation, possibly of cell interconnections, is occurring in the visual system in addition to photoreceptor cell addition.

Feeding

The ability to perform fast optical pursuit of targets, such that eye movement velocity matches stimulus velocity, is not possible until the time of increased optomotor response (Fishman, 1977). Such refinement of visual processing is necessary for the efficient localization and capture of prey items (Drost, 1987). Although larval fish are able to feed, they are often described as bumping into food before they mediate an attack (Hunter, 1972). Thus, it is apparent that development of the optokinetic response is closely related to the developmental stage of the retina and visual function.

When feeding on plankton, juvenile fish utilize a highly systematic search behavior termed *saltatory search* (Evans and O'Brien, 1988). The fish stop to search, detecting small plankton present in the visual field. The efficiency of such a search pattern would presumably be augmented by the increase of the optokinetic response.

Rod-mediated vision also extends the activity of organisms into lower light regimes at the cost of reduced acuity. There may instead be an enhancement of motion detection as evidenced by the optomotor responses. Ali (1959) noted that the feed-

ing behavior of young salmon changed dramatically when the light intensity dropped below the cone threshold. Above the cone threshold, the salmon exhibited typical planktivorous feeding behavior, whereas below the cone threshold, fish remained near the bottom of the tank, locating prey by silhouette and motion, dashing upwards to capture prey and then returning to the bottom. Below the rod threshold, visual feeding ceased.

Thus, changes in the teleost retina characteristic of the appearance of rods are paralleled by easily identified changes in behavior. This tightly correlated interdependence of life history strategy, behavioral change, and visual system transformation offers an exciting paradigm for future research.

TAXONOMIC DISTRIBUTION OF METAMORPHOSING FISH SPECIES

True metamorphosis occurs in lampreys and teleosts, and like the amphibians, all species that metamorphose experience a dramatic change in habitat and life-style corresponding to their growth from larvae to adults (Cohen, 1984). Metamorphosis is not known to occur in hagfish, elasmobranchs, lungfish, sturgeons, gars, or bowfins. Figure 5 illustrates the phylogenetic relationships among major groups of fish, and highlights specific orders within teleosts that are known to undergo metamorphosis. Possibly when the early life history of more members of these groups becomes known, species with indirect development and hence metamorphosis may be discovered. The following brief description provides details about the extent of the transformations that are known to occur in each order.

Petromyzontiformes

In the mountain brook lamprey (*Ichthyomyzon greeleyi*), metamorphosis consists of seven phases that take 100–140 days for completion. Larval lamprey are toothless and blind-burrowing filter feeders, whereas the adults have teeth, lateral eyes, and a large disc-shaped mouth. The major somatic changes at metamorphosis include development of the eyes and lateral line system and the transformation of the oral hood into the oral disc in the parasitic forms (William, Beamish, and Medland, 1988). The sea-lamprey (*Petromyzon marinus*) is also blind as an ammocoete larvae with its rudimentary eyes buried in the head. After 4–5 years as

a larvae, it metamorphoses with the appearance of well-formed eyes (Wald, 1957).

Elopomorpha

The elopomorphs, a superorder of primitive teleost fishes, includes the orders Anguilliformes, Elopiformes, and Notacanthiformes (eels, bonefish, and halosaurs, respectively, Nelson, 1984). All members of this group have a leptocephalus larval stage, which is marine-planktonic, and metamorphoses into the juvenile morph, which is pelagic in coastal regions. In the eels, metamorphosis accompanies the migration from the ocean into freshwater. Three phases are recognized in the development of the elopomorphs (Pfeiler, 1986). Phase 1, the premetamorphic phase following hatching, is a growth period ranging from 3 months in *Megalops* spp. (Smith, 1980 in Pfeiler, 1986) to 3 years in *Anguilla* spp. The yolk sac is small and resorbed 1–2 weeks after hatching. At the end of phase 1, the larvae reach their maximum size, of 50–100 mm, although some have been reported to reach 1.8 m (Nelson, 1984). During phase 2, the larvae metamorphose to the juvenile morph during which time the swim bladder develops, the pelvic fins appear, the medial fins and anus move forward, and the body size is greatly reduced. The retina of the very early stages of eels have not yet been examined; however, the ultrastructure of 50-mm specimens suggests that at this point, the retina is pure rod (Pankhurst, 1984). In phase 3, the postmetamorphic retina contains both rods and cones, suggesting that the cones arise at metamorphosis (Es-Sounni and Ali, 1985). This is in contrast to other teleosts where cones arise first and then rods appear at metamorphosis. Further studies of such a complete reversal of the developmental timing of rods and cones may help our understanding of the phylogenetic history of the vertebrate retina.

Clupeiformes

The clupeids, composed of the anchovies, herrings, pilchards, and sardines are well studied because of their great economic importance as a fisheries resource. The eggs are either pelagic and small, or demersal and large. Larvae hatching from pelagic eggs tend to be less developed with unpigmented eyes. Larger demersal eggs give rise to larvae at a more advanced developmental stage with pigmented eyes (McGowan and Berry, 1984). Larval life in the herring lasts from 3–6 months

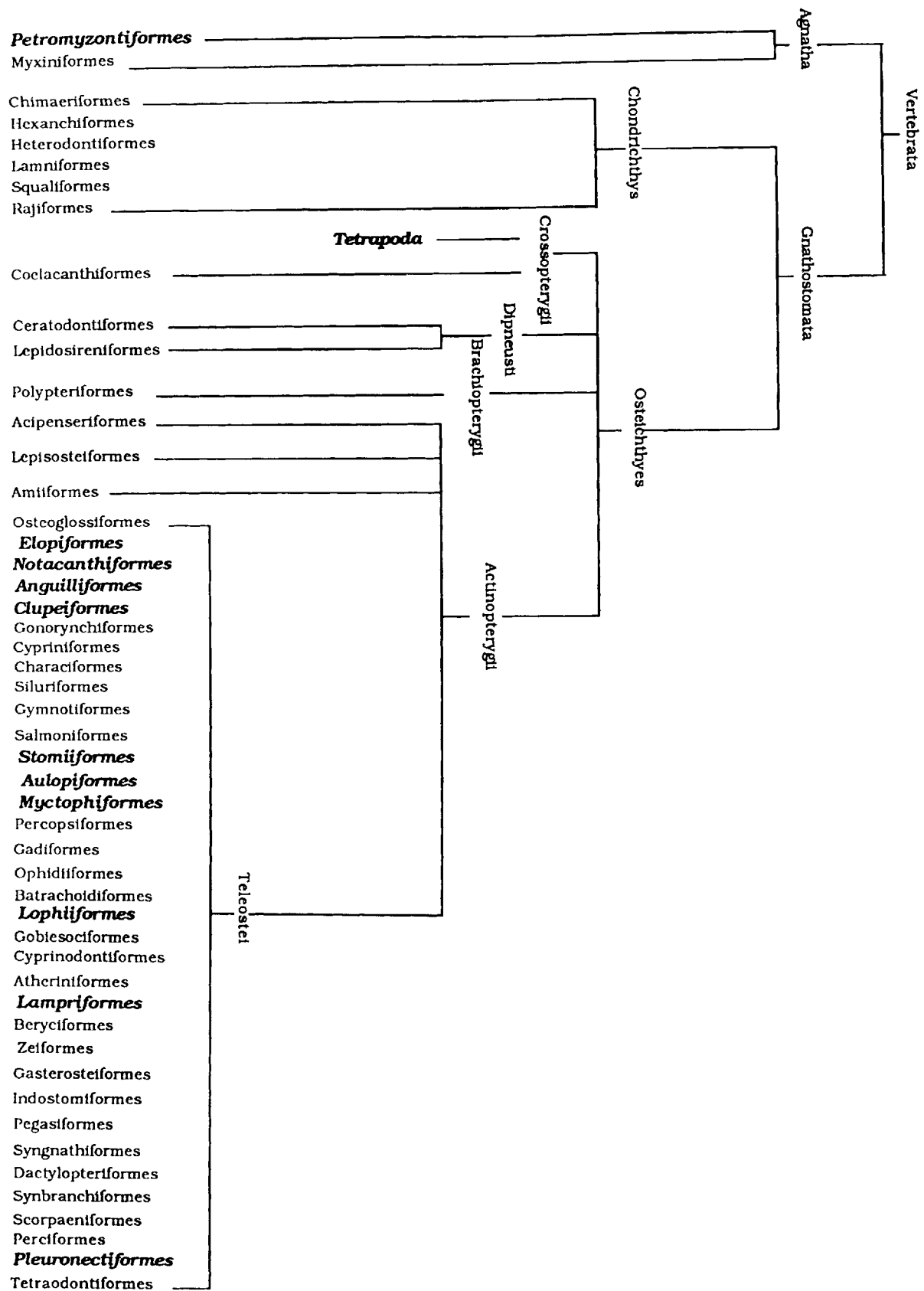


Figure 5 Phylogenetic relationships between vertebrates with metamorphosis. Within vertebrates, true metamorphosis is known to occur in lampreys and teleosts. The Orders that possess metamorphosing species are highlighted in bold italics. The presence of metamorpho-

(Blaxter and Jones, 1967). At ca. 20 mm, clupeids undergo metamorphosis at which time the position of the gut and the dorsal and anal fins shift forward relative to myomere 9. The pelvic fin also moves posteriorly in *Clupea harengus*. The retina of larval herring is pure cone, with the rods not appearing until metamorphosis (Blaxter and Jones, 1967). At this time the animals leave the plankton and begin to school (Blaxter and Hunter, 1982).

Stomiiformes

The hatchet fish, *Argyropspectus*, goes through a metamorphosis at which time the larval eyes transform from a normal configuration to a tubular morphology (Fig. 3) (Contino, 1939). The tubular eye has short rods in its dorsal retina and longer rods in its ventral retina (Ali and Anctil, 1976). The viperfish, *Chauliodus sloani*, also displays an indirect, metamorphic ontogeny with a marked decrease in size during metamorphosis (Kawaguchi and Moser, 1984; Balon, 1985). In several species of gonostomatid lightfishes, the formation of photophores occurs during a rapid metamorphosis. Lightfish are possibly the most prolific group of fishes known (Ahlstrom, 1974).

Scopelomorpha

The superorder Scopelomorpha, including the orders Aulopiformes and Myctophiformes, has many species that metamorphose. The adults have tubular eyes in *Benthalbella* and *Scopelarchus*, which are believed to develop at metamorphosis (Fig. 3) (Johnson, 1984a). Metamorphosis may be rapid in Ipnopinae beginning when eye plaques form. The larvae occur in the surface waters, whereas the adults are benthic and deep sea (Okiyama, 1984). In three genera, the adult eye is minute, however, in *Ipnops*, the eye is large and directed dorsally with no lens (Nelson, 1984). In the Myctophidae (lanternfish), the adult retina is pure rod with a degenerate pigmented epithelium (P.E.), whereas the P.E. is normal in the larvae (Johnson, 1984a; Ali and Anctil, 1976).

The giganturid family is deep mesopelagic or bathypelagic as adults and juveniles (Nelson, 1984). In the premetamorphic state, the eyes of giganturids are small, round, and directed later-

ally. The larvae remain unchanged until they are ca. 30–35 mm at which point they undergo an abrupt transformation. At this time, the eyes transform to a tubular morphology directed forward, parallel to the body axis (Fig. 3). Larvae differ so markedly from the juveniles that they were classified as separate species until recently (Johnson, 1984b). The extent of the morphological changes reflect a major change in the behavior of the adult relative to the larvae. Although the young are epipelagic planktonic, the adults apparently hang vertically, deep in the water column looking upwards for prey with their tubular eyes (Johnson, 1984b).

Lophiiformes

Ceratioid anglerfish differ from other lophiiformes due to their unique and extreme sexual dimorphism, which arises at metamorphosis (Marshall, 1971). The males are dwarfed, lack an external illicium, and have denticular teeth adapted to attach to the female. In the Linophrynidae, the deep-sea angler fish, found at 2000 m or more, the adult males have tubular eyes. Female eyes grow little after metamorphosis (Bertelson, 1951 in Marshall, 1971). There is no sign of eye degeneration although other species of deep-sea fish do have regressed eyes. After metamorphosis, ceratioid males acquire a highly developed sense of smell. The adult olfactory organ has a broad stack of sensory papillae with well-developed olfactory bulbs, nerves, and forebrain. In contrast, the females have minute papillae in the olfactory organs and regressed olfactory bulbs, nerves, and forebrain areas (Marshall, 1971; Bertelson, 1984).

Lampriformes

Early life history is not well known for many lampriform taxa. Development is gradual in most lampriformes but the transformation is abrupt in the trachipterids and has been termed a *metamorphosis* in several species such as *Desmodema*, *Trachipterus* (Olney, 1984), and *Stylophorus* (Rosenblatt and Butler, 1977). In the ribbonfish, *Desmodema lorum*, the young have a gas bladder and are believed to be epipelagic. The adults are thought to dwell at several hundred meters in a

head-up orientation. In adults, the lateral line extends the whole length of the tail and may act as a low-frequency sound antenna to sense predators below the visual field (Rosenblatt and Butler, 1977).

Stylophorus chordatus, the thread tail, undergoes a rapid metamorphosis and is a marine abyssal species as an adult. Like *Desmodema*, the lateral line extends onto the exceedingly long, caudal filament (Rosenblatt and Butler, 1977). The adult has tubular eyes directed forward and is assumed to maintain a vertical orientation in the water. This mode of life is thought to be common in trachipterids. Instead of developing tubular eyes, *Trachipterus* has been observed to have an elongation of the pupil ahead of the lens producing an aphakic space which functions to increase light entering the eye. The eye itself can rotate 90°, presumably to facilitate both vertical and horizontal orientations of the body (Haedrich, 1974).

Pleuronectiformes

The flatfish are perhaps the best known examples of metamorphosing species. The bilaterally symmetrical larvae, which is planktonic, switches to a benthic habitat at the end of the larval stage and transforms to the asymmetrical form at metamorphosis. At this time, one eye migrates to the contralateral side of the body and the body becomes pigmented (Ahlstrom, Amaoka, Hensley, Moser, and Sumida, 1984). The larval eye has a pure-cone retina until prior to metamorphosis when rods begin to appear (Sandy and Blaxter, 1980).

Flounders also exhibit a change in their dorsal light response during their metamorphosis to a laterally compressed morphology (Neave, 1985). Dorsal light response of plaice and turbot is similar to other species prior to metamorphosis suggesting similar balance mechanisms compromising between light and static orientation cues (Neave, 1985; von Holst, 1935). After metamorphosis, light influences balance to only one-quarter the extent of gravity, and the upright position shifts away from vertical, attributable to eye migration. In the postmetamorphic animal, the sacculi and lagenae are used as gravity sensors instead of sound sensors, suggesting that efferents from the midbrain visual centers to the otolith organs inhibit the utriculi and excite the sacculi and lagenae (Platt, 1973b in Neave, 1985).

CONCLUSIONS

The selective advantage of metamorphosis is presumably to allow life in a new habitat where fac-

tors such as reduced competition and predation, or greater food resources result in a higher probability of survival. Metamorphosis is widespread amongst fish species and should be considered as one of many developmental strategies that have continued plasticity as a common theme. Postembryonic development and change appears to be the rule rather than the exception in teleost fish species as it is in amphibia. Even in species without specific identifiable metamorphic events, development continues throughout the life of the animal, albeit at a slower pace. For example, in adult teleosts, as the retina grows through cell addition and stretching, rods continue to be added throughout the retina (Fernald, 1989). We should perhaps view metamorphosis as another type of nonembryonic development that occurs in a relatively short time frame, making it a more obvious event in the animal's lifetime.

Metamorphosis has been of interest to evolutionary biologists as an adaptation, but also to developmental biologists because events occur in sizeable animals allowing access to parts of the developmental program which are inaccessible in embryos of higher vertebrates. It is possible in principle to use metamorphic change to gain access to mechanisms through which extracellular factors effect changes in gene expression. Wald (1981) suggested that metamorphosing animals might have two distinct developmental programs occurring in parallel within one organism, each regulated by its own genetic programs. Because metamorphic events trigger synthesis of DNA, RNA, and proteins, which can be traced with molecular techniques, this hypothesis about metamorphosis could now be tested directly. The addition of rods to the visual system is an obvious place to use genetic analyses to understand the mechanisms at work. The fact that indirectly developing species have larvae with a pure-cone retina with rods not arising until metamorphosis provides a natural experimental paradigm.

During ontogeny of the vertebrate retina, cone photoreceptors always develop before rods, but there is considerable variation in the timing of rod addition. In teleost fish, this variability is extreme (Fig. 1). Species with *direct* development, which hatch into animals resembling miniature adults, add rods shortly after cones during embryonic development, whereas species with a larval development stage often do not add rods until weeks later. There has been no prior attempt to account for this pattern of staggered photoreceptor addition. The temporal correlation between rod neurogenesis and metamorphosis in species with indirect

development, and the early appearance of rods in species that lack a larval stage, suggest an order to the variability in the timing of rod appearance among teleosts.

The relatively late appearance of rod photoreceptors in development is true throughout vertebrate phylogeny (Fernald, 1989) and is thought to reflect the evolutionary sequence of vertebrate photoreceptor origins. Occasionally rod outer segments have been observed to develop before cone outer segments, but in these cases, the cone nuclei arise first (Kahn, 1974). Biological innovations appear typically at the end of ontogeny so that characters which arise at, or after metamorphosis are likely to be phylogenetically more recent than characters which precede metamorphosis (Freeman, 1982; Gould, 1982). Given these data, it seems likely that rods may have evolved in conjunction with the metamorphosis from the larval to the juvenile stage of indirectly developing fishes. During evolution, the contraction and/or loss of the larval stage has resulted in earlier appearance of rod photoreceptors during development, but always after cones. As originally suggested from their ontogeny, Walls (1942) proposed that cones are phylogenetically older than rods, and that rods have evolved several different times.

Metamorphic change in this large number of species offers tantalizing natural experiments. Altered behavioral performance can be identified relative to specific environmental changes and the corresponding cellular and genetic systems responsible then isolated. Such natural connections between behavioral ecology and visual performance are a rich, future resource for neurobiologists.

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